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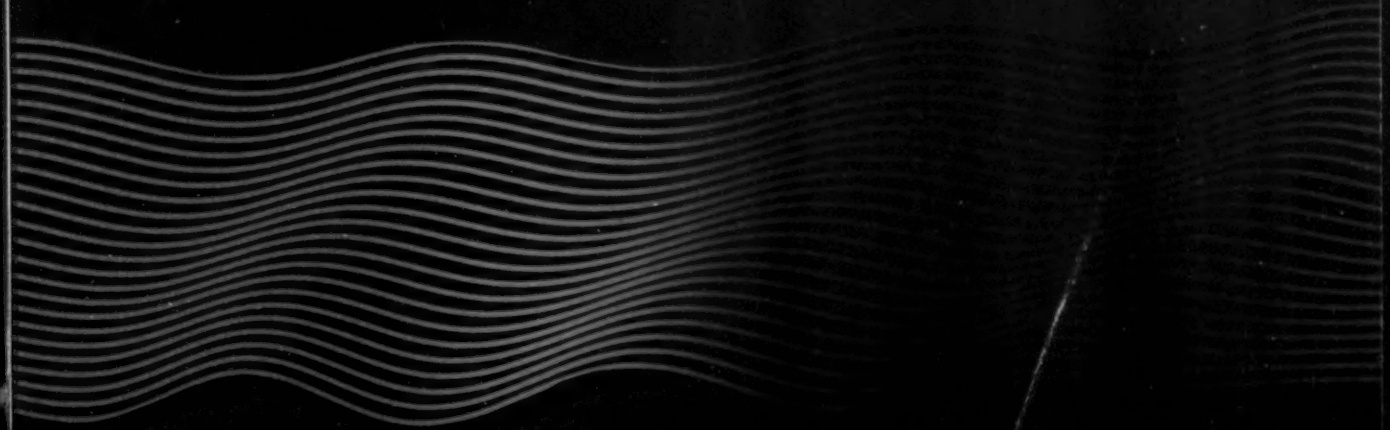

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Among-taxon congruence in biodiversity patterns: can stream insect diversity be predicted using single taxonomic groups?

Jani Heino, Timo Muotka, Riku Paavola, and Lauri Paasivirta

Abstract: The utility of single taxonomic groups as indicators of biodiversity variation in other taxa has recently gained increasing attention, but such studies on stream organisms are lacking. We studied the diversity patterns of mayflies, stoneflies, caddisflies, and chironomid midges across 110 headwater streams in Finland. Specifically, we examined if species richness and assemblage composition showed similar variation among the taxonomic groups across environmental gradients and if a single taxon could be used as a predictor of diversity in the other groups. Species richness and composition in different taxa exhibited slightly different relationships to environmental gradients, leading to low degrees of concordance. The diversity of mayflies and chironomids showed strongest relationships with stream acidity and water colour, whereas stoneflies and caddisflies exhibited more complex correlations with geographical location and local environmental variables. The overall assemblage composition, however, exhibited significant among-taxon congruence, as shown by Mantel tests. However, even these correlations remained rather low, thus limiting their potential for conservation purposes. Overall, our results do not support the use of single taxonomic groups as indicators of insect biodiversity in headwater stream ecosystems. Alternative approaches for lotic biodiversity assessment (e.g., morphospecies, higher-taxon richness, and environmental diversity) should thus be examined in future studies.

Résumé : L'utilisation d'un seul groupe taxonomique pour refléter la variation de la biodiversité des autres taxons suscite de plus en plus d'intérêt ces derniers temps, mais aucune étude du genre n'a été faite sur les organismes des eaux courantes. Nous avons examiné les patterns de diversité des éphéméroptères, des plécoptères, des trichoptères et des diptères chironomidés de 110 cours d'eau d'amont de Finlande. En particulier, nous avons examiné si la richesse en espèces et la composition des peuplements varient de façon similaire d'un groupe taxonomique à l'autre le long de gradients environnementaux et si l'analyse d'un seul groupe taxonomique peut servir à prédire la diversité des autres groupes. La richesse en espèces et la composition des divers taxons varient de façon légèrement différente d'après les gradients environnementaux, si bien que la concordance est faible entre les taxons. La diversité des éphéméroptères et des chironomidés possède les relations les plus fortes avec l'acidité et la couleur de l'eau, alors que les plécoptères et les trichoptères ont des corrélations plus complexes avec la position géographique et les variables locales de l'environnement. La composition générale de la communauté montre, toutefois, une congruence significative entre les taxons, comme l'indiquent des tests de Mandel. Cependant, même ces corrélations restent assez faibles, ce qui limite leur potentiel à servir à des fins de conservation. En général, nos résultats ne justifient pas l'utilisation d'un seul groupe taxonomique comme indicateur de la biodiversité de l'ensemble des insectes dans les écosystèmes d'amont d'eau courante. Dans des études futures, on devra donc examiner des méthodes de rechange pour évaluer la biodiversité en eau courante (e.g., les espèces morphologiques, la richesse des taxons de niveau supérieur et la diversité environnementale).

[Traduit par la Rédaction]

Introduction

Biodiversity surveys and conservation evaluation would greatly benefit from effective biodiversity indicators, i.e., taxonomic groups that reflect the diversity of other organisms across a set of environments, thus acting as surrogates for "wholesale" biodiversity (Gaston 1996*a*; McGeoch 1998). The conservation value of an area is typically judged using a measure of species richness, or some variant of it, in well-known taxonomic groups (Gaston 1996*b*; Angermeier and

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Winston 1997), yet rigorous tests of the robustness and generality of these taxa as biodiversity indicators are largely lacking. Given that many, if not most, taxonomic groups remain poorly known, much of the biological diversity present in an area may go unnoticed and does not contribute to the measure of its conservation value (Gaston 2000). However, because relatively little is known about the degree of among-taxon congruence in diversity patterns, judgements based on a few well-known taxonomic groups may lead to erroneous conclusions about the conservation value of an area (see Reid 1998).

The degree to which different taxonomic groups show congruent diversity patterns has been studied intensively (for reviews, see Gaston and Williams (1996); Flather et al. (1997), and Gaston (2000)) but still remains poorly known for many ecosystems. Species richness in different taxonomic groups usually exhibits highest covariation at biogeographical and regional scales (Reid 1998; Ricketts et al. 1999; Heino 2002), but congruence is often weaker at smaller scales (Prendergast and Eversham 1997; Reid 1998) and diminishes further when local systems are compared (Allen et al. 1999*a*; Ricketts et al. 2002). The lack of strong congruence at local scales is unfortunate, because in practice, it is at the level of habitats and landscapes that most conservation and management programs are likely to be conducted (Niemelä 1997; Prendergast et al. 1999; Kerr et al. 2000). Furthermore, rather than focusing on mere species richness, it might be more instructive to consider the overall patterns in assemblage composition. Then, a different view may emerge; for example, various freshwater groups have been shown to exhibit significant covariation in assemblage structure across local systems (Allen et al. 1999*b*; Kilgour and Barton 1999; Paszkowski and Tonn 2000).

Surveys of stream invertebrate biodiversity usually concentrate on easily identifiable taxonomic groups, such as mayflies, stoneflies, and caddisflies, but neglect more diverse groups (e.g., chironomid midges) if these require expertise knowledge. Yet, without knowledge on the degree of congruence among various groups, decisions about the conservation value of a stream are based only on well-known "indicator" taxa. However, if a species-rich group omitted from the analyses does not covary with more well-known taxonomic groups, an inherent bias will be incorporated in conservation decisions.

We studied congruence in the diversity patterns of insect taxa dominant in boreal headwater streams, i.e., mayflies, stoneflies, caddisflies, and chironomid midges. Our aim was to examine whether these taxonomic groups show congruent diversity patterns across local stream systems, and if so, are these generated by similar responses of different taxa to major environmental gradients. Specifically, we tested whether the diversity of a speciose, but often neglected, group of insects, chironomid midges, could be reliably predicted based on information from better-known insect groups. Furthermore, we examined the influence of spatial extent on the degree of among-taxon congruence in species richness and assemblage composition by stratifying our data by ecoregion. Our data spanned very long environmental gradients at both across- and within-ecoregion scales (see also Heino et al. 2002), providing scope for strong among-taxon congruence in diversity patterns. Based on findings from previous studies, however, these four groups are known to exhibit highly variable responses to water chemistry and temperature (e.g., Wiggins and Mackay 1978; Ward 1992), potentially leading to contrasting diversity patterns across headwater streams. We concentrated on near-pristine headwater streams because (*i*) their biota remains poorly known, (*ii*) they harbour characteristic macroinvertebrate assemblages different from those in larger rivers (e.g., Malmqvist and Hoffsten 2000), and (*iii*) they are extremely vulnerable to landscape alteration by forestry activities (e.g., Vuori et al. 1998) and thus require immediate conservation efforts.

Materials and methods

Study area and field sampling

We sampled riffle sites in 110 streams across Finland (60–70°N, 25–32°E). Finland is divided into five ecoregions (Alalammi and Karlson 1988; see also Heino et al. 2002), four of which were included in this study. Thus, we randomly sampled streams in south boreal (n = 18 streams), middle boreal (n = 29), north boreal (n = 38), and arctic–alpine (n = 25) ecoregions. As we concentrated on near-pristine headwater streams (orders 1 to 3, base flow < 0.6 $m^3 \cdot s^{-1}$), lake outlets, spring-fed streams, and streams with obvious human influence were avoided. Further, streams were selected based on their accessibility, i.e., only streams within 2 km from the nearest road were included.

Several riparian and in-stream variables were measured at each site. The tree species composition and integrity of the riparian zone (i.e., percentage of riparian zone without human impact) were assessed along both shores in a 50-m section directly upstream of the sampling site. Shading by overhanging vegetation was measured as percent canopy cover at 20 locations in evenly spaced, cross-channel transects covering the whole study section. Depth and current velocity (at 0.4 × depth) were measured at 40 random locations along the same transects. Moss cover and substrate size distribution were assessed at 10 randomly spaced 50 cm × 50 cm quadrats. Visual estimates of the percent cover of 10 particle size classes, ranging from organic matter (0) to large boulder (9) (see Table 1), were made for each quadrat. These estimates were subsequently averaged to give a mean particle size for a site. Mean stream width was also measured at each sampling site.

Water samples were collected simultaneously with benthic sampling and were analyzed for pH, alkalinity, conductivity, total nitrogen [TN], total phosphorus [TP], colour, and iron [Fe] by regional environment centres of Finland, using national standards.

Aquatic insects were sampled between early September and late October in 1998. Additional material from 1994 was also included if the sampling methods were identical to those used in 1998. At each site, we took a 2-min kick-net (net mesh size 0.3 mm) sample covering most microhabitats present in a riffle of ~100 m^2. Animals and associated material were immediately preserved in 70% alcohol. The insects were mostly identified to species level. For some early-instar larvae and some chironomids (mainly Tanypodinae, 13% of all chironomid taxa), however, the lowest feasible taxon was genus.

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Table 1. Means, standard deviations (SD), and ranges of the environmental variables and species richness of each taxonomic group in the 110 study sites.

Variable	Mean	SD	Minimum	Maximum
Colour (mg $Pt \cdot L^{-1}$)	123	131	5	600
Iron ($\mu g \cdot L^{-1}$)	1135	1413	5	6000
Total nitrogen ($\mu g \cdot L^{-1}$)	354	262	32	1200
Total phosphorus ($\mu g \cdot L^{-1}$)	20	22	0	140
pH	6.8	0.8	4.7	8.4
Alkalinity ($mmol \cdot L^{-1}$)	0.30	0.35	0	1.88
Conductivity ($mS \cdot m^{-1}$)	4.78	3.48	0.94	19.90
Current velocity ($m \cdot s^{-1}$)	0.36	0.12	0.12	0.73
Stream width (m)	3.1	2.0	0.6	10.0
Particle size[a]	5.7	1.5	0.8	8.2
Depth (cm)	23	8	9	45
Shading (%)	45	23	0	91
Moss cover (%)	27	25	0	93
Mayflies	3.8	2.4	0	8
Stoneflies	5.3	2.4	0	11
Caddisflies	4.7	2.6	1	12
Chironomids	4.7	2.4	1	12

[a]Substrate size was averaged for each site based on visual estimates of the percentage cover of 10 substrate classes: (0) organic matter to (1) sand (diameter 0.25–2 mm), (2) fine gravel (2–6 mm), (3) coarse gravel (6–16 mm), (4) small pebble (16–32 mm), (5) large pebble (32–64 mm), (6) small cobble (64–128 mm), (7) large cobble (128–256 mm), (8) boulder (256–400 mm), and (9) large boulder and bedrock (>400 mm).

Statistical methods

Environmental variables were subjected to principal components analysis (PCA) with varimax rotation (e.g., Legendre and Legendre 1998) to describe major gradients in environmental conditions across the streams. If necessary, appropriate transformations were performed to approximate normal distributions. The site scores on each principal component were subsequently used as independent variables in regression analyses.

Detrended correspondence analysis (DCA) was used to describe the major pattern of change in species composition among sites. Gradient length of the first DCA axis describes the degree of species turnover: sites separated by a gradient length of more than 4 standard deviation (SD) units have no species in common (Gauch 1982; Legendre and Legendre 1998). DCA based on the presence–absence data for each taxonomic group were run using PC-Ord (McCune and Mefford 1999). Sites with no species in a taxonomic group were omitted from the DCA analyses. Site scores on the first DCA axis were used as a dependent variable in subsequent regression analyses. Because of the controversy surrounding the use of DCA, especially regarding detrending of the second axis (see Legendre and Legendre 1998), only the first axis was considered in this study.

Several measures of turnover diversity were derived to determine which insect group showed most variability across the streams. We used the total inertia of the DCA as an index of overall variability for each taxonomic group (see Ohmann and Spies 1998). Two indices of β diversity were also calculated for each taxonomic group. The original β diversity index of Whittaker (1960) was calculated using the formula $\beta_W = (S/\alpha) - 1$, where S is the total number of taxa in a data set and α is mean number of taxa recorded at a single site. We also calculated another index for each taxonomic group following Harrison et al. (1992): $\beta_2 = (S/\alpha_{max} - 1)/(N - 1) \times 100$, where S is the total number of taxa in a data set, α_{max} is the maximum number of taxa recorded at a single site, and N is the number of sites. Thus, β_2 ranges from 0 to 100 and measures the degree by which regional diversity exceeds the maximum local diversity. One of the benefits of this modified index is that it distinguishes between true species turnover and simple gradual variation in α diversity (Harrison et al. 1992).

Stepwise regression analysis was used to model variation in species richness (α diversity) and species composition among the streams for each insect group. This method takes independent variables (here, site scores on each principal component and on latitude and longitude) in the model, in order of importance, according to how much of the variation in the dependent variable they explain. Furthermore, Spearman's rank correlations were calculated to assess covariation in species richness and species composition (DCA axis 1 scores; Allen et al. 1999*b*). In addition to pairwise correlations among taxonomic groups, we also used Spearman's rank correlations to test the utility of each group as an indicator of richness of the other groups combined, i.e., overall insect species richness. All tests were two-tailed, because for predictive purposes, a strong negative relationship can be as useful as a strong positive one (Prendergast and Eversham 1997). It is important to notice, however, that because our data are not strictly independent, i.e., they are spatially autocorrelated, standard tests of significance must be interpreted cautiously (e.g., Carroll and Pearson 1998). Therefore, we emphasize the strengths of the environmental diversity and among-taxon relationships (i.e., coefficients of determination and correlation coefficients) more than statistical significance and associated p values. To reduce the effects of any latitudinal gradients in species richness, the

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Table 2. Summary of principal components analysis of the environmental data.

	Component			
	PC1	PC2	PC3	PC4
Eigenvalue	4.427	2.590	1.936	1.028
Percentage variation explained	34.051	19.896	14.907	7.907
Colour	**0.957**[a]	–0.110	–0.022	–0.022
Iron	**0.932**[a]	–0.018	–0.030	0.014
Total nitrogen	**0.909**[a]	–0.064	0.014	–0.229
Total phosphorus	**0.909**[a]	–0.083	–0.039	0.250
pH	**–0.637**	**0.656**	0.084	0.034
Alkalinity	–0.117	**0.953**[a]	–0.025	0.020
Conductivity	0.070	**0.922**[a]	0.057	–0.033
Current velocity	0.071	–0.065	**0.793**	–0.015
Stream width	0.042	0.062	**0.783**[a]	0.217
Particle size	–0.342	0.004	**0.648**	–0.053
Depth	0.367	0.154	**0.591**[a]	0.367
Shading	0.264	–0.441	**–0.503**	0.074
Moss cover	–0.057	–0.040	0.125	**0.927**

Note: Variables with the highest loadings (>0.50) on each principal component (PC) are given in bold.

[a]Logarithmic transformation.

among-taxon correlations were recalculated at the ecoregion level, i.e., separately for each of the four ecoregions.

Finally, the overall assemblage congruence was assessed using the Mantel test, which examines the null hypothesis of no concordance between two distance matrices. The strength of the relationship is measured by the standardized Mantel statistic r_M, which is identical to Pearson's correlation coefficient, ranging from –1 to 1 (McCune and Mefford 1999). We used Sorensen's coefficient to construct the distance matrices on the presence–absence data for each taxonomic group. The significance of the pairwise relationships between matrices was assessed using a Monte Carlo permutation procedure with 1000 permutations. Mantel tests were run using PC-Ord (McCune and Mefford 1999). Sites with no species in a taxonomic group were omitted, leaving 99 sites for the analyses. Pairwise Mantel tests were also run separately within each of the four ecoregions.

Results

Our study sites spanned a wide range of environmental variability present in boreal headwater streams. For example, pH varied from 4.7 to 8.4, water colour varied from 5 to 600 mg $Pt \cdot L^{-1}$, canopy cover varied from 0% to 91%, and moss cover varied from 0% to 93%. PCA on environmental data generated four components with eigenvalues > 1.0, collectively explaining 76.7% of variation in the original variables (Table 2). Water colour, iron, [TN], and [TP] had high positive loadings, and pH a high negative loading on the first principal component. The second component represented a gradient of stream acidity, with high loadings for alkalinity, conductivity, and pH. The third component was related to stream size and heterogeneity, as indicated by high loadings for many in-stream variables (current velocity, stream width, particle size, and depth) and riparian shading. The fourth component was mainly related to moss cover (Table 2).

In total, our samples contained 23 mayfly (Ephemeroptera), 29 stonefly (Plecoptera), 54 caddisfly (Trichoptera), and 72 chironomid (Diptera, Chironomidae) taxa. The mean and range of the taxon number per site for each taxonomic group are given in Table 1. Environmental gradients related to species richness differed between the taxonomic groups (Table 3). The number of mayfly species showed the strongest relationship to PC2 (acidity gradient), and the regression model including this variable and PC1 (water colour) explained almost 50% of variation in mayfly richness. Species richness of stoneflies was only weakly related to any of the environmental gradients, and the model incorporating latitude and PC4 (moss cover) explained only 8.6% of variation. The model best explaining caddisfly species richness incorporated five variables, accounting for 38.6% of variation. Latitude, the first variable to enter this model, was negatively related to the number of caddisfly species. Species richness of chironomids showed a weak (3.8% of variation explained), albeit significant, relationship to PC2 (acidity) (Table 3).

The first DCA axis generally explained only a minor portion of total variation, but gradient lengths indicated considerable turnover in species composition (Table 4). Total inertia from DCA analyses, as well as β diversity indices, showed that turnover across sites was highest for chironomids, followed by caddisflies, mayflies, and stoneflies (Table 4).

Environmental gradients explaining variation in species composition, as indicated by the DCA axis scores, varied among the taxa groups (Table 5). Site scores on the first axis of the mayfly DCA showed the strongest relationship with PC1 (water colour), followed by PC2 (acidity), and longitude. This model accounted for 41.7% of variation in mayfly species composition. For stoneflies, latitude and PC3 (stream size) together explained 24.1% of variation in species composition. The model explaining caddisfly species composition incorporated four variables and accounted for 28.0% of variation. The species composition of chironomids was

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Table 3. Regression models for the relationship between environmental gradients and richness for each taxonomic group.

Dependent variable	Independent variables	Coefficient	R^2	p
Mayflies	Constant	3.827		
	PC2 (acidity)	1.039	0.194	
	PC1 (water colour)	–1.000	0.374	
	PC3 (stream size)	0.782	0.484	<0.001
Stoneflies	Constant	–6.754		
	Latitude	0.002	0.048	
	PC4 (moss cover)	0.480	0.086	0.008
Caddisflies	Constant	31.096		
	Latitude	–0.006	0.204	
	PC3 (stream size)	0.616	0.277	
	PC1 (water colour)	–0.901	0.317	
	Longitude	0.005	0.358	
	PC4 (moss cover)	0.438	0.386	<0.001
Chironomids	Constant	4.918		
	PC2 (acidity)	0.195	0.038	0.041

Note: R^2 denotes cumulative coefficient of determination; PC, principal component, see Table 2.

Table 4. Summary of detrended correspondence analysis (DCA) for each taxonomic group.

Taxon	Eigenvalue	Gradient length	Variance explained	Total inertia	β_W diversity	β_2 diversity
Mayflies	0.576	4.023	14.9	3.872	5.05	1.72
Stoneflies	0.353	3.839	9.1	3.862	4.47	1.50
Caddisflies	0.579	5.503	6.8	8.488	10.48	3.21
Chironomids	0.583	5.312	4.7	12.293	14.32	4.59

Note: Eigenvalue, gradient length, and percentage variance explained by the first axis, as well as total inertia, are given. Also shown are the indices of β diversity, calculated following Whittaker (1960; β_W) and Harrison et al. (1992; β_2).

Table 5. Regression models for the relationships between environmental gradients and species composition for each taxonomic group.

Dependent variable	Independent variables	Coefficient	R^2	p
Mayflies	Constant	–4.359		
	PC1 (water colour)	0.491	0.281	
	PC2 (acidity)	–0.301	0.367	
	Longitude	0.002	0.417	<0.001
Stoneflies	Constant	7.666		
	Latitude	–0.008	0.180	
	PC3 (stream size)	–0.175	0.241	<0.001
Caddisflies	Constant	2.134		
	PC3 (stream size)	–0.297	0.128	
	PC2 (acidity)	–0.208	0.191	
	PC1 (water colour)	0.184	0.240	
	PC4 (moss cover)	–0.164	0.280	<0.001
Chironomids	Constant	3.247		
	PC1 (water colour)	0.494	0.336	<0.001

Note: Scores on the first axis of detrended correspondence analysis (DCA) were used to describe major patterns of species composition. R^2 denotes cumulative coefficient of determination; PC, principal component, see Table 2.

mainly related to PC1 (water colour), explaining 33.6% of variation (Table 5).

Congruence of diversity patterns among the taxonomic groups was generally weak, although some pairwise relationships were statistically significant. For species richness, among-taxon correlations ranged from 0.061 to 0.290, and only three of the relationships were significant (Fig. 1). Furthermore, correlations between species richness of each group and that of the other groups combined exhibited similarly low congruence, with coefficients varying from 0.147 for caddisflies ($p = 0.125$) to 0.349 for mayflies ($p < 0.01$). For species composition, among-taxon correlations were somewhat higher, varying from 0.168 to 0.532. The highest correlations were between mayflies and chironomids and between

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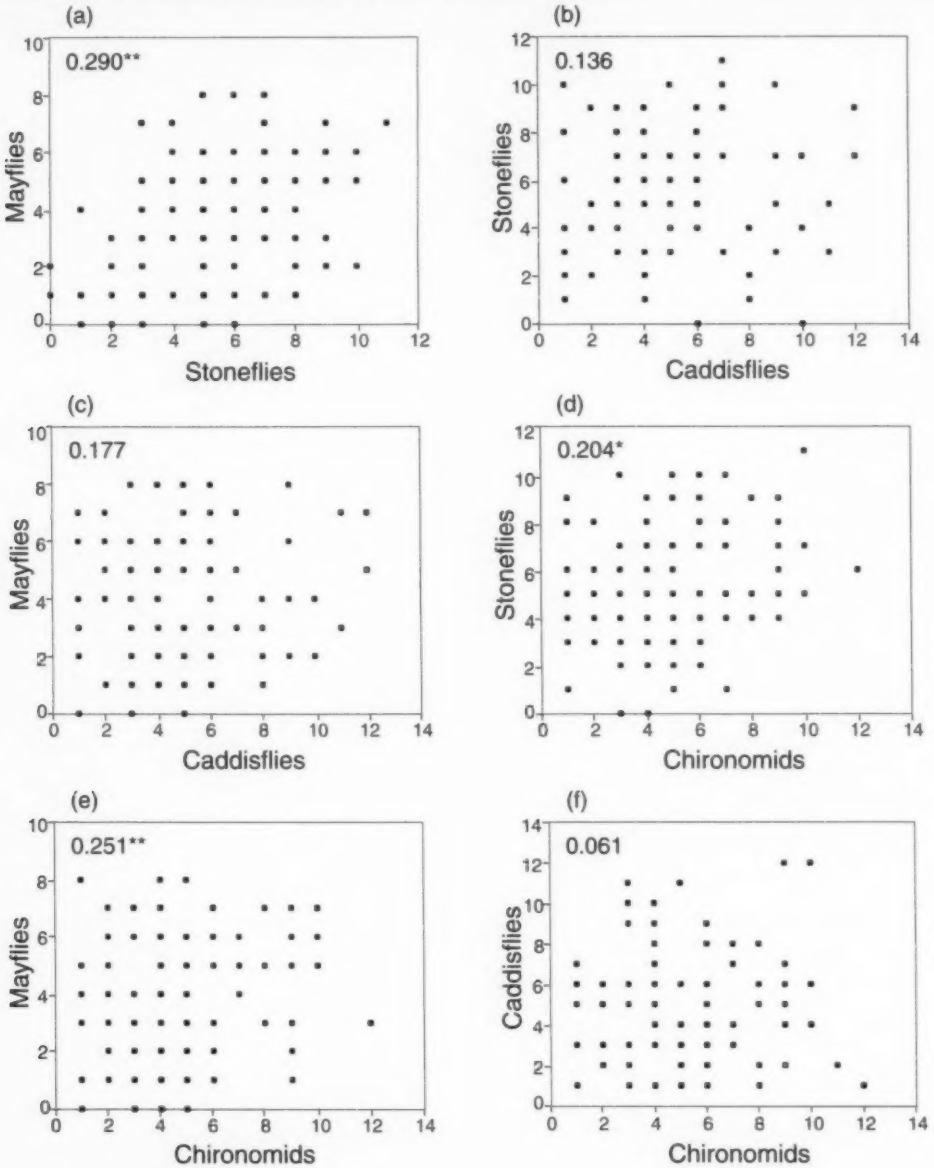
Fig 1. Congruence in species richness among the four groups of stream insects studied. Congruence was tested using Spearman's rank correlations, and figures refer to correlation coefficients (r_s). *, $P < 0.05$; **, $P < 0.01$.



stoneflies and caddisflies. Although four of the six correlations were statistically significant ($p < 0.05$), plots of pairwise relationships showed wide scatter (Fig. 2).

Despite low covariation in species richness and composition, the overall patterns of assemblage composition exhibited significant concordance. According to Mantel tests, most pairwise comparisons were highly significant (Monte Carlo test, $p = 0.001$), and even the weakest relationships, those between mayflies and stoneflies ($p = 0.023$) and between mayflies and chironomids ($p = 0.030$), were significant. However, albeit significant, Mantel's r_M statistic remained generally low, ranging from 0.10 to 0.23.

Patterns at the within-ecoregion level paralleled those at the broader extent of analysis, i.e., congruence was variable and mainly low, in terms of both species richness and assemblage composition. Pairwise relationships were, however, somewhat stronger at the within-ecoregion level (Tables 6 and 7). For species richness, the highest correlations occurred between mayflies and stoneflies and between mayflies and caddisflies in the south boreal ecoregion and between mayflies and chironomids in the middle boreal ecoregion. All other pairwise correlations were weak ($r_S < 0.50$) and mainly nonsignificant (Table 6). Similarly, although some pairwise Mantel tests were significant, the associated values

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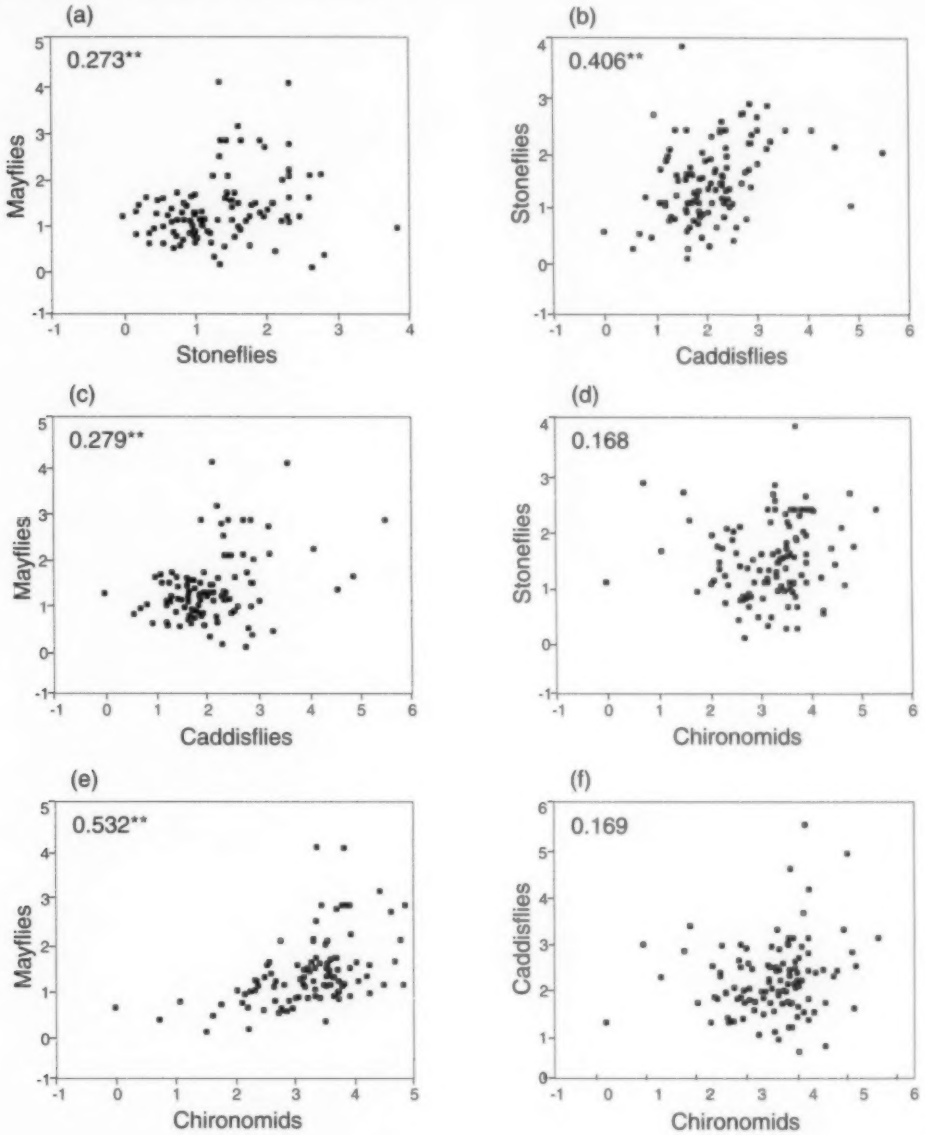
Fig 2. Congruence of spatial variation in the turnover diversity of the groups studied. Site scores on the first axis of detrended correspondence analysis were used as an index of species turnover. Congruence was tested using Spearman's rank correlations, and figures refer to correlation coefficients (r_s). *, $P < 0.05$; **, $P < 0.01$.



of r_M remained low ($r_M < 0.50$), the only exception being the relationship between mayflies and caddisflies in the south boreal ecoregion (Table 7).

Discussion

Recent studies on the congruence of diversity patterns among taxonomic groups have yielded variable results. Although studies conducted on large biogeographic scales may show relatively strong congruence (e.g., Ricketts et al. 1999), those at smaller scales or across local habitats typically report low degrees of covariation among different taxonomic groups (e.g., Allen et al. 1999*a*). Because practical conservation planning typically focuses on local habitats, e.g., individual stream reaches and their riparian settings, low among-taxon congruence at the level of local systems renders the use of indicator taxa somewhat questionable (Balmford et al. 1996*b*; Prendergast et al. 1999; Kerr et al. 2000).

We found generally weak congruence in species richness and assemblage composition among the four aquatic insect groups dominant in boreal streams. Although we did find significant correlations for some taxa pairs, there was considerable variability about these relationships. Therefore, our

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Table 6. Spearman's rank correlations for congruence in richness among different taxonomic groups at the within-ecoregion level and all ecoregions combined.

	Ecoregion									
	South boreal (18 sites)		Middle boreal (29 sites)		North boreal (38 sites)		Arctic–alpine (25 sites)		Combined (110 sites)	
Comparison	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p
Mayflies vs. stoneflies	**0.597**	0.009	0.249	0.192	0.122	0.466	0.261	0.207	0.290	0.002
Mayflies vs. caddisflies	**0.617**	0.006	0.389	0.037	0.196	0.238	0.444	0.026	0.177	0.065
Mayflies vs. chironomids	0.388	0.112	**0.561**	0.002	–0.055	0.741	0.200	0.339	0.251	0.008
Stoneflies vs. caddisflies	0.048	0.849	0.382	0.041	0.222	0.181	0.225	0.281	0.136	0.156
Stoneflies vs. chironomids	0.220	0.380	0.196	0.309	0.067	0.688	0.305	0.138	0.204	0.032
Caddisflies vs. chironomids	0.302	0.223	0.373	0.046	–0.242	0.144	0.285	0.167	0.061	0.525

Note: The highest correlations ($r_s > 0.50$) are shown in bold.

Table 7. Results of Mantel tests for pairwise comparisons of congruence in assemblage composition among different taxonomic groups at the within-ecoregion level and all ecoregions combined.

	Ecoregion									
	South boreal (17 sites)		Middle boreal (21 sites)		North boreal (36 sites)		Arctic–alpine (25 sites)		Combined (99 sites)	
Comparison	r_M	p	r_M	p	r_M	p	r_M	p	r_M	p
Mayflies vs. stoneflies	0.068	0.300	0.068	0.233	0.324	0.001	0.338	0.004	0.114	0.023
Mayflies vs. caddisflies	**0.557**	0.003	0.238	0.033	0.231	0.012	0.210	0.016	0.218	<0.001
Mayflies vs. chironomids	0.175	0.094	0.308	0.004	0.090	0.119	0.202	0.028	0.099	0.030
Stoneflies vs. caddisflies	–0.003	0.598	0.084	0.184	0.332	0.002	0.181	0.052	0.230	<0.001
Stoneflies vs. chironomids	0.039	0.382	–0.084	0.200	0.094	0.147	0.235	0.016	0.117	0.004
Caddisflies vs. chironomids	0.373	0.002	0.429	0.001	0.119	0.083	0.108	0.140	0.166	<0.001

Note: The highest correlation coefficients ($r_M > 0.50$) are shown in bold.

analyses provide little support for the use of single indicator taxa in biodiversity inventories of headwater streams. It must be borne in mind, however, that our analyses were not planned to give recommendations on the use of surrogate taxa to identify sets of priority sites for protection. Instead, we were interested in testing whether different insect taxa could be used as indicators of overall diversity in spatially extensive stream biodiversity surveys. It is possible that despite low among-taxon congruence in species richness and assemblage composition, complementarity-based priority sites identified through indicator taxa may capture the overall regional species diversity quite well, as demonstrated by Howard et al. (1998) for tropical forests in Uganda. The explanation for the strong among-taxon congruence in site complementarity was that Uganda encompasses highly heterogeneous land areas and each taxonomic group exhibits similar distribution patterns across these biogeographic gradients (Howard et al. 1998). This, however, clearly is not the case for stream organisms in the boreal landscapes of Finland, where some aquatic taxa (e.g., stoneflies) exhibit geographical diversity trends distinctly different from those of most other groups (Heino 2002; Heino et al. 2002).

Mechanisms creating significant among-taxon congruence in diversity patterns may be classified into four groups (Gaston and Williams 1996). Congruence may stem from (*i*) random draw of taxa from the regional species pool, (*ii*) similar responses of different taxa to the same environmental gradient, (*iii*) spatial covariance in factors independently accounting for diversity variation in different taxa, or (*iv*) biotic interactions among taxa. Of these, among-taxon differences in (*i*) and (*ii*) are the most likely explanations for the relatively low congruence in the present study. Further, inconsistent sampling effort may affect patterns of congruence (Gaston 2000), but this should not plague our study because all streams were sampled using similar, strictly standardized techniques.

The size of the regional species pool may greatly influence the number of species in local assemblages: local species richness usually increases with increasing number of species in the regional pool (Cornell and Lawton 1992; Huston 1999). Therefore, if regional diversity patterns covary and the relationship between regional and local richness is similar among taxonomic groups, then diversity patterns can be expected to be concordant also at the local scale (Gaston 2000). This may indeed be one of the reasons why the congruence in species richness was low in this study. For instance, the species richness of stoneflies was positively related to latitude, whereas that of caddisflies exhibited an opposite latitudinal trend. For mayflies and chironomids, no consistent geographical diversity patterns were detected. Nevertheless, for lotic macroinvertebrate assemblages as a whole, local species richness may still be positively related to regional species richness (Heino et al. 2003).

Among-taxon congruence in diversity patterns could also arise from similar responses by different taxa to major environmental gradients (Gaston and Williams 1996). In our study, however, each insect group responded to slightly different environmental gradients, as shown by the environmental-

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diversity regressions. The diversity of stream invertebrates is correlated with numerous environmental factors, of which stream size, habitat heterogeneity, and water chemistry are generally the most important ones (Vinson and Hawkins 1998). These factors were also important for the insect groups studied here, but the key environmental gradients differed among taxonomic groups. For mayflies and chironomids, species richness and composition were negatively related to gradients in water acidity and water colour, whereas stoneflies and caddisflies showed more complex relationships to geographical location and local environmental factors. Furthermore, the proportion of variation explained was very low for stoneflies and chironomids, implying that factors not measured here are affecting these taxa. These patterns concur with the findings of previous studies showing that mayflies are sensitive to acidity, whereas stoneflies are relatively acid-tolerant but largely inclined towards cold-water streams in their distributions. By contrast, caddisflies comprise a heterogeneous group of species with regard to their responses to environmental factors, including stream temperature (Wiggins and Mackay 1978; Ward 1992).

Although biotic interactions may also create among-taxon congruence, their importance is likely to be minor in the present context. Each of the insect groups studied incorporates a wide range of trophic modes. Mayflies are mainly algal scrapers or gatherers, whereas most stoneflies are either predators or shredding detritivores. The feeding strategies of caddisflies and chironomid midges vary even more widely (Merritt and Cummins 1996). Such versatility in trophic modes within a single taxonomic group may prevent the formation of strong among-taxon congruence. Explaining spatial congruence in diversity patterns in terms of biotic interactions seems thus inapplicable to stream insects if purely taxonomic entities are compared.

The four taxonomic groups studied here exhibited somewhat differing β diversities across the sampling sites. Not surprisingly, chironomids, the most diverse of the groups, exhibited the highest turnover among sites, followed by caddisflies. By contrast, mayflies and stoneflies showed relatively low levels of β diversity. Differences in β diversity could, in theory, relate to the potential use of a taxonomic group as a biodiversity indicator (Oliver et al. 1998). A group showing high β diversity should reflect the overall environmental variation more closely than one with low β diversity and should thus capture variation in other taxa more effectively. This was not quite the case in our study, where chironomids and caddisflies were no better than mayflies or stoneflies in predicting the variation of diversity of other taxa. The most parsimonious explanation for this finding is that the environmental gradients to which the four groups respond are too different to allow any strong predictions of the diversity variation in other taxa groups to be made. Similarly, Oliver et al. (1998) found low similarity in β diversity and species turnover patterns among terrestrial plant, invertebrate, and vertebrate taxa, suggesting low utility of single taxonomic groups as biodiversity indicators in Australian forests.

Despite the generally low congruence of species richness and species composition, the overall community patterns of different taxonomic groups exhibited generally significant concordance, as shown by Mantel tests and associated Monte Carlo permutations. This suggests that if only a single insect group is to be used in biodiversity inventories of headwater streams, attention should be paid to overall patterns in assemblage composition, not merely to a single measure of species richness. This is also suggested by other studies on freshwater ecosystems, which typically report concordant community patterns among various taxonomic groups (Allen et al. 1999*b*; Kilgour and Barton 1999; Pazkowski and Tonn 2000). However, it must be stressed that for conservation purposes, the explanatory power of pairwise relationships is far more important than the mere statistical significance (Flather et al. 1997; Gaston 2000), and the level of assemblage concordance among the four taxonomic groups studied here was overall rather low.

To conclude, congruence in diversity patterns was generally low and variable among the four aquatic insect groups studied, at both scales of analysis (i.e., within and across ecoregions). At the first glance, this may seem frustrating, because species-level information is often extremely costly to obtain (e.g., Lawton et al. 1998). At coarser spatial scales, more congruence in taxa distributions might have been detected (e.g., Weaver 1995), but because many conservation decisions are made at the level of landscapes and local habitats, this is the scale at which effective surrogate approaches are most urgently needed (Prendergast and Eversham 1997; Ricketts et al. 2002). Alternative surrogate measures proposed for other ecosystems and taxonomic groups are, for example, the use of morphospecies, higher-taxon richness (Balmford et al. 1996*a*, 1996*b*), and environmental diversity (Faith and Walker 1996). Of these, the use of higher taxa bears most promise for stream ecosystems, because genus- and family-level identifications have been successfully used in stream biomonitoring programs (Bowman and Bailey 1998; Bailey et al. 2001). Furthermore, our study touched only a small fraction of the biodiversity present in freshwater environments. Obviously, further attempts to test the effectiveness of surrogate approaches in capturing freshwater biodiversity should incorporate a wider array of organisms, including periphytic algae, aquatic macrophytes, and fish. Nevertheless, one would expect the strongest congruence to occur among closely related and approximately similar-sized organisms (Gaston 1996*a*; Fleishman et al. 2000). Although lotic macroinvertebrates do not constitute an ecologically homogeneous group, they certainly are more similar to each other than to other aquatic organisms that likely respond to their environment in profoundly different ways. Overall, our results suggest that there is little scope for the use of surrogate taxa in stream biodiversity assessment. It therefore appears that there is no short cut for extensive species-based surveys incorporating a wide array of species with different ecologies if we are to satisfactorily manage the biodiversity in freshwater environments.

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The influence of hatchery coho salmon (*Oncorhynchus kisutch*) on the productivity of wild coho salmon populations in Oregon coastal basins

Thomas Nickelson

Abstract: To aid in the recovery of depressed wild salmon populations, the operation of hatcheries must be changed to reduce interactions of juvenile hatchery fish with wild fish. Evidence suggests that productivity of wild populations can be reduced by the presence of large numbers of hatchery smolts in lower rivers and estuaries that attract predators. An index of productivity based on the density-independent rate of reproduction of wild coho salmon (*Oncorhynchus kisutch*) in 12 Oregon coastal river basins and two lake basins was negatively correlated with the average number of hatchery coho salmon smolts released in each basin. The index of productivity was not significantly correlated with the average proportion of hatchery coho salmon in each naturally spawning population or with habitat quality. Alterations to hatchery programs that could encourage recovery of wild populations include (*i*) avoiding release of large numbers of smolts in areas with high concentrations of wild fish, (*ii*) decreasing the number of smolts released, and (*iii*) using a volitional release strategy or a strategy that employs smaller release groups spread temporally.

Résumé : Pour favoriser la récupération des populations en déclin de saumons sauvages, il faudrait modifier le fonctionnement des piscicultures de façon à réduire les interactions entre les jeunes poissons de pisciculture et les poissons sauvages. Il y a des indications que la productivité des populations sauvages peut être réduite dans les rivières d'aval et les estuaires par la présence de grands nombres de saumoneaux de pisciculture qui attirent les prédateurs. Un indice de productivité basé sur le taux de reproduction indépendant de la densité de saumons coho (*Oncorhynchus kisutch*) sauvages dans 12 systèmes hydrographiques de rivières côtières et dans deux lacs de l'Oregon est en corrélation négative avec le nombre moyen de saumoneaux coho de pisciculture libérés dans chaque bassin versant. L'indice de productivité n'est pas en corrélation significative avec le pourcentage moyen de saumons coho de pisciculture présents dans chaque population naturelle reproductrice, ni avec la qualité de l'habitat. Les changements dans la programmation des piscicultures qui pourraient favoriser la récupération des populations sauvages comprennent les mesures suivantes : (*i*) ne pas relâcher de grands nombre de saumoneaux dans les régions qui possèdent déjà des concentrations élevées de poissons sauvages, (*ii*) réduire le nombre de saumoneaux libérés et (*iii*) utiliser une stratégie de libération raisonnée ou une stratégie de libération impliquant des groupes plus petits sur une période de temps plus longue.

[Traduit par la Rédaction]

Introduction

Since the early 1980s, the use of hatcheries to produce salmon (*Oncorhynchus* sp. and *Salmo salar*) has increased dramatically (McNeil 1983; Isaksson 1988; Anderson 1997). This increase has occurred in watersheds bordering both the Pacific and Atlantic oceans and adjacent seas. The roles of these hatcheries range from private-for-profit net-pen farms and salmon ranches (in which fish are released to the sea) to publicly funded facilities that produce fish to support commercial and recreational fisheries or to aid in the recovery of endangered wild populations. Unfortunately, the operations of these facilities often result in conflicts with production and management of natural salmon stocks (McNeil 1991).

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The role of hatcheries is an important consideration in planning the recovery of wild anadromous salmonids. Hatcheries could play a positive role in the recovery of wild populations through the supplementation of spawning populations. More typically, hatchery fish are seen as a risk to the genetic integrity of wild populations (Hindar et al. 1991; Currens et al. 1997; Clifford et al. 1998). In addition, a number of recent papers discuss potential ecological effects of hatchery fish interactions with wild fish (e.g., Einum and Fleming 2001; Levin et al. 2001; Levin and Williams 2002).

In reviewing the status of coho salmon (*Oncorhynchus kisutch*) on the west coast of the United States, Weitkamp et al. (1995) concluded that hatchery fish pose a threat to the genetic integrity of wild fish. Further, "widespread hatchery production of coho salmon" was cited as a significant factor in their conclusion that wild coho salmon in the Oregon Coast evolutionarily significant unit (ESU) were "likely to become endangered".

Hatcheries have been present in the streams of the Oregon Coast ESU since the early twentieth century (Lichatowich 1999). Fish released in the early years were primarily fry and fingerling and it was not until the 1960s that smolts became the primary product. Production of yearling smolts

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Table 1. Populations listed geographically north to south with pertinent data used in the analyses.

	Parameter estimates					
Basin	α	*r*	*p*	Proportion hatchery spawners	Average number of smolts released	Habitat index
Necanicum River	3.89	–0.73	0.060	0.41	0	0.04
Nehalem River	2.96	–0.65	0.110	0.57	668 612	0.26
Tillamook Bay	2.18	–0.72	0.068	0.72	628 533	0.05
Nestucca River	4.82	–0.80	0.032	0.30	6 118	0.10
Salmon River	2.95	–0.52	0.230	0.88	320 729	0.07
Siletz River	2.04	–0.81	0.027	0.76	401 103	0.31
Yaquina River	7.79	–0.88	0.009	0.28	165 157	0.43
Alsea River	1.64	–0.84	0.017	0.20	962 238	0.38
Siuslaw River	9.24	–0.79	0.036	0.34	57 698	0.36
Siltcoos Lake	7.13	–0.85	0.015	0.08	0	1.00
Umpqua River	4.06	–0.71	0.074	0.18	293 281	0.15
Tenmile Lakes	3.92	–0.79	0.034	0.00	47 695	1.00
Coos River	7.18	–0.74	0.059	0.10	85 512	0.27
Coquille River	2.78	–0.74	0.057	0.06	76 125	0.09

Note: The correlation coefficients (*r*) and *p* values refer to the regression results used to calculate α. For all of these regressions, $N = 7$.

from coastal hatcheries peaked at about 10 million fish in the early 1980s (Pacific Fisheries Management Council (PFMC) 2002), from about a dozen hatcheries, including two large private salmon ranches. However, by 1992, these ranches had gone out of business because of poor returns (Lichatowich 1999). At the time of the status review in the mid-1990s, production of coho salmon smolts from public hatcheries was 4–5 million fish.

The purpose of this paper is to explore the extent to which hatchery programs in the Oregon Coast ESU may affect recovery of depressed populations of wild coho salmon. To accomplish this, I analyzed the population dynamics of wild populations of coho salmon with varying degrees of potential interaction with hatchery fish. The analysis addressed two primary hypotheses: (1) productivity of the wild population is related to the proportion of hatchery fish in the spawning population and (2) productivity of the wild population of a basin is related to the number of hatchery smolts released into the basin. An alternate hypothesis was also addressed: productivity of the wild population of a basin is related to the quality of habitat in the basin.

Methods and materials

Coho salmon life history

To analyze the population dynamics of coho salmon, one must understand their life history in Oregon coastal basins. Adult coho salmon typically spawn in late fall and winter, with most smolts (>95%) migrating to the ocean in their second spring. About 20% of a cohort return to spawn as precocious males (jacks) after their first summer at sea (Nickelson and Lawson 1998). The remainder of the cohort return as adults after their second summer at sea. Thus, the spawning population in any given year is composed of fish from two cohorts and the recruits of a given brood return 2 and 3 years after spawning.

Population parameters

Fourteen populations of wild coho salmon (Table 1) inhabiting river and lake basins between the Columbia River and Cape Blanco (also known as the Oregon Coast ESU) were included in this analysis. Twelve of the basins had active coho salmon hatchery programs during all or part of the study period. Basin-scale estimates of wild coho salmon spawner abundances (for both jacks and adults) are available for Oregon coastal basins since 1990. Population estimates for the 12 river basin and two lake basin populations are based on expansion of spawning surveys at randomly selected sites and standard sites, respectively (Jacobs et al. 2002). Estimates of wild adults were expanded to preharvest abundance by dividing by one minus the annual fishery exploitation rate for wild coho (PFMC 2002). Total recruits resulting from spawning of wild jacks and adults in year t were calculated by adding the estimated abundance of wild jacks returning in year $t + 2$ to the preharvest estimate of wild adults in year $t + 3$. Estimates of recruits per spawner were calculated for each brood t.

Index of productivity

For the purpose of this paper, the productivity of a population was defined as the density-independent rate of reproduction, the average number of mature progeny per spawner that occurs at very low spawner abundance (Ricker 1975). Typically, recruits per spawner increases as spawner abundance decreases because of density-dependent processes. Thus, to effectively use recruits per spawner as an index of productivity across populations, it should be calculated over a similar range of spawner density and environmental conditions. To minimize the effects of environmental variability on the indices, data for only the 1990–1996 brood years were used. This was a period of consistently poor marine survival for Oregon coho salmon ranging from 0.5% to 1.1% (average 0.7%, standard deviation 0.002) for hatchery fish (Curt Melcher, Oregon Department of Fish and Wildlife (ODFW), 17330 Southeast Evelyn Street, Clackamas, OR 97015, un-

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published data). Calculation of the density-independent rate of reproduction in effect standardizes recruits per spawner for the effects of spawner density.

The density-independent rate of reproduction (α) was calculated from a Ricker stock–recruit relationship (Ricker 1975) of the form

$$R = \alpha P e^{-\beta P}$$

Parameters were estimated for each population by fitting the linear form of the equation:

$$\ln(R/P) = \ln(\alpha) - \beta P$$

using least squares regression analysis where ln is the natural logarithm, R is the number of naturally produced recruits, P is the number of wild parent spawners (hatchery spawners were not included), and β is a parameter with dimensions $1/P$.

Potential factors influencing productivity

The influence of hatchery fish on the productivity of wild coho salmon populations was tested using two different measures of hatchery fish: the proportion of hatchery fish in the natural spawning population and the number of hatchery smolts released in each basin. In addition, because habitat affects survival of wild coho salmon (Solazzi et al. 2000), an index of the quality of the habitat in each basin was also tested for its relationship to wild population productivity.

The proportion of hatchery fish in the natural spawning population of each basin was based on analysis of scales collected from carcasses found on the spawning grounds. Scale pattern recognition was used to differentiate hatchery from wild fish using a modification of methods originally developed by Scarnecchia and Wagner (1980). The scale pattern of a wild coho salmon is characterized by an obvious freshwater annulus near the center of the scale, whereas the pattern of a hatchery coho salmon is characterized by a vague freshwater annulus relatively far from the center of the scale. The freshwater annulus on the scale from a wild fish is typically followed by several more widely spaced circuli ending at a vague ocean entrance check, whereas that of a typical hatchery scale pattern is followed by circuli with spacing similar to that of circuli before the annulus and an ocean entrance check that is often strong. In addition, hatchery smolts are usually larger than wild smolts at ocean entrance and therefore have a greater distance and a higher circuli count from the center of the scale to the freshwater annulus and to the ocean entrance check. Blind tests of scale pattern recognition of known samples have resulted in 95% of scales from hatchery fish and 85% of scales from wild fish being correctly classified. The average annual proportion of hatchery spawners in each population was estimated from data for the parent years 1990–1996 (L. Borgerson, ODFW, 28655 Hwy. 34, Corvallis, OR 97333, unpublished data).

The average number of coho salmon smolts released in each basin was calculated from ODFW hatchery records (M. Lewis, ODFW, 28655 Hwy. 34, Corvallis, OR 97333, unpublished data). Smolt release years 1992–1998 were used, corresponding to the 1990–1996 brood years and 1993–1999 adult return years.

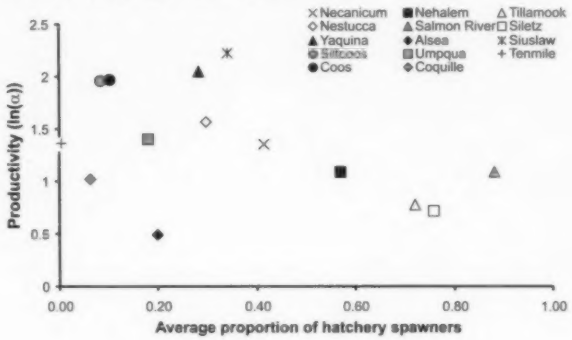

Fig. 1. Relationship between productivity of wild coho salmon (*Oncorhynchus kisutch*) and average proportion of hatchery spawners in the naturally spawning population. α is the density-independent rate of reproduction calculated assuming recruits were the offspring of wild spawners only.

Habitat quality was indexed as the proportion of high-quality habitat as estimated from habitat surveys (Moore et al. 1997) and a coho habitat model (Nickelson 1998). This model is based on the quantity and quality of winter habitat. Habitat capacity predicted from the model has been related to freshwater survival of coho salmon. High-quality habitat is defined as that habitat in which freshwater survival is high enough that a marine survival of 3% will result in at least replacement of the population (Nickelson 1998). The two lake basins were assumed to have 100% high-quality habitat because the lakes should be able to provide winter habitat adequate to result in a high survival rate for the juvenile fish produced in the stream habitat of the basins.

Regression analysis

Univariate regressions were used to determine the relationships between the index of population productivity and (1) the average proportion of hatchery fish in the naturally spawning population, (2) the average number of hatchery smolts released in the basin, and (3) the habitat quality index. The natural log of α was used to provide a straight-line form to the regression equations.

When calculating the index of productivity, the regression coefficients of 2 of the 14 populations were not significant at $p \leq 0.10$. All regressions were repeated leaving these two populations out of the data set to be sure that they did not significantly influence the results.

Results

Productivity (α) of the wild coho salmon populations ranged from less than two to greater than nine recruits per spawner (Table 1). Productivity was not significantly related ($p = 0.123$) to the proportion of hatchery fish in the naturally spawning population (Fig. 1). However, the relationship between productivity and the average number of smolts released had a highly significant negative slope ($R^2 = 0.53$, $p = 0.003$; Table 2 and Fig. 2). The proportion of high-quality habitat in each basin was not related ($p = 0.256$) to productivity of the wild coho salmon populations (Fig. 3).

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Table 2. Correlations between productivity of wild coho salmon in Oregon coastal streams and three independent variables listing number of populations (n), and regression intercept (a), slope (b), correlation coefficient (r), and p value.

Independent variable	Data set	n	a	b	r	p
Proportion hatchery spawners	All basins	14	1.65	–0.82	–0.43	0.127
Average annual smolts released	All basins	14	1.71	–0.13	–0.73	0.003
Proportion high quality habitat	All basins	14	1.18	0.56	0.33	0.256
Proportion hatchery spawners	All basins with $p \leq 0.10$	12	1.67	–0.92	–0.39	0.208
Average annual smolts released	All basins with $p \leq 0.10$	12	1.73	–0.14	–0.73	0.007
Proportion high quality habitat	All basins with $p \leq 0.10$	12	1.23	0.51	0.29	0.353

Fig. 2. Relationship between productivity of wild coho salmon (*Oncorhynchus kisutch*) and average number of hatchery smolts released in the respective basins. α is the density-independent rate of reproduction calculated assuming recruits were the offspring of wild spawners only. The legend is the same as for Fig. 1.

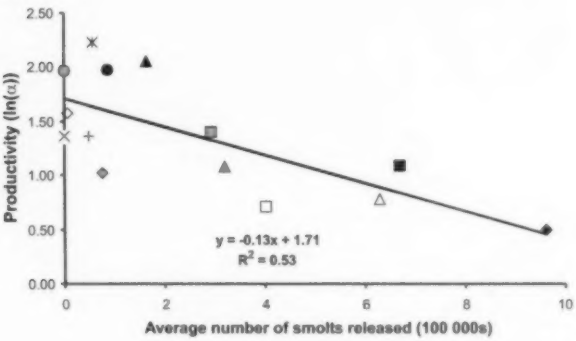
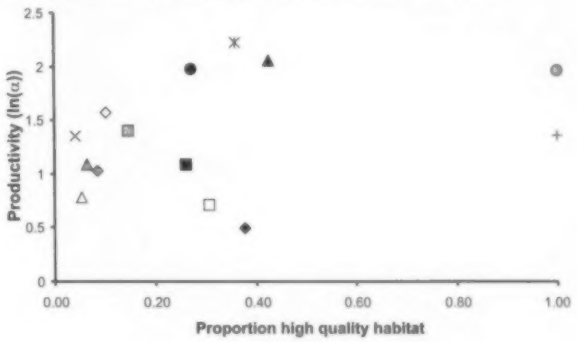


Fig. 3. Relationship between productivity of wild coho salmon (*Oncorhynchus kisutch*) and the estimated proportion of high-quality habitat in each basin. α is the density-independent rate of reproduction calculated assuming recruits were the offspring of wild spawners only. The legend is the same as for Fig. 1.



Regression analyses using only those populations in which the index of productivity was estimated with $p \leq 0.10$ provided results similar to those using all populations (Table 2). This was particularly true for the relationship between productivity and smolts, as the correlation coefficient was the same and p value was slightly higher because of the smaller sample size.

Discussion

An index of productivity based on the density-independent rate of reproduction for wild coho salmon in 12 Oregon coastal river basins and two lake basins was negatively correlated with the average number of hatchery coho salmon smolts released in each basin. This relationship held for a subset of the data that omitted basins in which productivity was estimated with poor precision, which reinforces the validity of the relationship. The methods used in this analysis are based on the assumption that hatchery fish contribute no offspring to the recruits. This is consistent with a literature review by Fleming and Petersson (2001), which found that hatchery fish seldom contribute to self-sustaining wild populations. In addition, analysis of hatchery steelhead (*Oncorhynchus mykiss*) in several Oregon streams suggests that their natural contribution rate is very low (Chilcote 2003). If this is not the case for hatchery coho salmon in Oregon coastal basins, this analysis underestimates the negative relationship between wild productivity and hatchery smolt releases. However, variation in success of hatchery spawners, either among basins or among years, would result in unpredictable changes to the outcome of this analysis.

An unexpected result was the lack of a relationship between habitat quality and productivity of wild populations. Coho salmon smolt production in Oregon coastal streams has been related to quality of winter habitat (Nickelson 1998; Solazzi et al. 2000), which was the basis for the habitat quality index used in these analyses. One possible explanation for the lack of a relationship is that the negative effects of hatchery fish on productivity masked the positive effects of habitat quality. Another possible explanation is that because this analysis encompassed a period of poor marine survival and relatively low abundance, wild populations in all basins were concentrated in stream reaches of high-quality habitat, as predicted by Nickelson and Lawson (1998). If this were the case, and lacking any effects of hatchery fish, differences in the density-independent rate of reproduction would not necessarily be apparent among basins with different quantities of high-quality habitat.

The above results suggest two questions. First, what are the mechanisms that cause the negative correlation between hatchery smolt releases and productivity of the wild populations? Second, what are the implications to recovery of wild coho salmon? The analyses conducted here do not provide an answer to the first question. However, when combined with the observations of others, they may provide some insight from which to speculate on probable mechanisms.

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Possible mechanisms of hatchery–wild interactions

As noted previously, hatchery fish can impact productivity through genetic effects resulting from interbreeding or through ecological effects. That the number of hatchery smolts released in a basin was significantly negatively correlated with productivity of wild coho salmon in the 14 basins, and the proportion of hatchery spawners was not, suggests that ecological rather than genetic interaction of hatchery and wild coho salmon is the most important mechanism affecting productivity of wild coho salmon on the Oregon Coast. The ecological interactions could take such forms as competition (McMichael et al. 1997; Flagg et al. 2000) or disease transmission (Mitchum et al. 1979). However, evidence suggests that the mechanism reducing productivity of wild coho salmon was more likely predation, in this case the attraction of predators to concentrations of hatchery and wild juveniles in coastal estuaries.

For this to be the case, predators must be attracted to concentrations of hatchery fish, and wild fish must be intermixed with the hatchery fish. Typically, the coho hatcheries on the Oregon coast during the study period released smolts in groups of 100 000 or more (Lewis 2002). Hillman and Mullan (1989) found that the release of hatchery chinook salmon caused juvenile wild chinook salmon to leave their normal habitat and join the school of hatchery fish that was migrating downstream. Similar behavior has also been suggested to occur in Atlantic salmon (Hansen and Jonsson 1985). Wild juvenile coho salmon have been observed intermixed with hatchery coho salmon in schools in the lower Alsea River estuary (R. Buckman, ODFW, 2040 S.E. Marine Science Dr., Newport, OR 97365, personal communication). Such behavior may make them more vulnerable to predation if predators are attracted by the presence of large numbers of hatchery fish.

Predators appear to target aggregations of hatchery salmonids. Harbor seals (*Phoca vitulina*; Brown and Mate 1983), spiny dogfish (*Squalus acanthias*; Beamish et al. 1992), northern pikeminnow (*Ptychocheilus oregonensis*; Collis et al. 1995), and Caspian terns (Collis et al. 2001; Ryan et al. 2003) appear to be attracted to concentrations of hatchery salmonids. Indeed, on the Oregon coast, predation has been identified as potentially being a major source of mortality for salmonid smolts in the Nehalem and Alsea basins. A study of radio-tagged smolts in the Nehalem Basin estimated mortality of hatchery coho salmon smolts from predation by birds and mammals to be about 50% in 1999, and losses of wild steelhead smolts to predators to be 54% in 2001 (C.B. Schreck, Oregon State University, Corvallis, OR 97331, unpublished data). Harbor seals and double-crested cormorants (*Phalacrocorax auriyus*) were the most abundant predators. Double-crested cormorants have also been implicated in predation on fingerling rainbow (*Oncorhynchus mykiss*) and cutthroat (*Oncorhynchus clarki*) trout in the North Platte River, Wyoming (Lovvorn et al. 1999). In the Alsea Basin, relative abundance of avian predators (primarily cormorants) and observed incidents of predation behavior by harbor seals declined sharply when releases of hatchery coho salmon were reduced from one million in 1997 to 200 000 in 1998 (R. Buckman, ODFW, 2040 S.E. Marine Science Dr., Newport, OR 97365, personal communication). These observations are pertinent because the productivity of the wild population of coho salmon in the Alsea Basin was by far the lowest of the 14 populations examined and the number of hatchery smolts released was by far the largest.

Implications for recovery

Most studies of interactions between hatchery and wild salmon have dwelt on the relative differences in success of hatchery fish versus wild fish in the natural environment (Reisenbichler and McIntyre 1977; Chilcote et al. 1986; Nickelson et al. 1986). Few studies have provided evidence of ecological interactions between hatchery and wild fish. Fresh (1997) provides limited examples of evidence for competition between hatchery and wild salmon and predation of hatchery salmon on wild salmon. More recently, Flagg et al. (2000) and Einum and Fleming (2001) conducted reviews of the ecological differences and interactions between hatchery and wild salmonids and the latter concluded, "many of the current stocking practices may be detrimental to the recipient populations". Levin et al. (2001) demonstrated that survival of wild chinook salmon in the Columbia Basin was negatively related to the number of hatchery chinook salmon released. Levin and Williams (2002) demonstrated a similar relationship between wild chinook salmon survival and the number of hatchery steelhead released. The results of the current study provide further evidence that large hatchery programs present risks to the recovery of populations of wild salmon through ecological interactions. This evidence suggests that the presence of large numbers of hatchery smolts during migration to the ocean (typical of smolt release programs for salmon and steelhead in the Pacific Northwest) results in increased mortality to wild smolts by attracting predators.

To aid recovery of depressed wild salmon, the operation of hatcheries must be changed to reduce interactions of hatchery smolts with wild smolts. The most effective option for reducing interactions between hatchery and wild salmon would be judicious siting of hatchery programs to avoid concentrations of wild fish. Hatchery programs designed for harvest augmentation should be removed from basins with habitat that has high potential to produce wild salmonids. Such hatcheries should be located in basins in which the potential of the habitat to produce wild salmonids is low. Where this is not feasible, decreasing the number of smolts released from hatcheries could reduce risks. For example, in the years following the period of this study, total production of hatchery coho salmon on the Oregon Coast was reduced to less than a million smolts, and as noted above, observations of predation on coho salmon smolts in the Alsea River declined when hatchery smolt numbers were reduced. The use of a volitional release strategy or a strategy that employs smaller release groups spread temporally are other options that may reduce the density of smolts in the lower portions of coastal rivers and, thus, interactions with wild fish.

The greater influence of hatchery fish on productivity of wild fish compared with the influence of habitat quality observed in this study does not reduce the importance of restoring habitat to the recovery of wild coho salmon. The influence of hatchery fish reinforces the importance of a multipronged approach to recovery. A program that reduces harvest, restores habitat, and reduces hatchery effects is necessary. Without a proactive approach to reduce the effects of

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hatchery releases on the productivity of wild salmon, recovery is likely to be significantly hampered, in some cases to the point of being unachievable.

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Relationship between natural productivity and the frequency of wild fish in mixed spawning populations of wild and hatchery steelhead (*Oncorhynchus mykiss*)

Mark W. Chilcote

Abstract: The proportion of wild fish in 12 mixed populations of hatchery and wild steelhead (*Oncorhynchus mykiss*) was evaluated for its relationship to mean and intrinsic measures of population productivity. The population mean of ln(recruits/spawner) was used to represent mean productivity. Intrinsic productivity was represented by values for the Ricker *a* parameter as estimated from fits of spawner and recruit data. Significant regressions ($p < 0.001$) were found between both measures of productivity and the proportion of wild fish in the spawning population (P_w). The slopes of the two regressions were not significantly different ($p = 0.55$) and defined a relationship suggesting that a spawning population comprised of equal numbers of hatchery and wild fish would produce 63% fewer recruits per spawner than one comprised entirely of wild fish. Study findings were not sensitive to likely levels of data error or confounded by extraneous habitat correlation with P_w. Population status assessments and conservation monitoring efforts should include P_w as a critical variable. For natural populations, removal rather than addition of hatchery fish may be the most effective strategy to improve productivity and resilience.

Résumé : La proportion de poissons sauvages dans 12 populations mixtes de truites arc-en-ciel anadromes (*Oncorhynchus mykiss)* sauvages et de pisciculture a été mise en relation avec des mesures de productivité moyenne et intrinsèque de la population. La moyenne de ln(recrues–reproducteurs) dans la population représente la productivité moyenne et les valeurs du paramètre *a* de Ricker calculées à partir d'ajustements des données sur les recrues et les reproducteurs, la productivité intrinsèque. Il existe des régressions significatives ($p < 0{,}001$) entre chacune des deux mesures de productivité et la proportion de poissons sauvages dans la population des reproducteurs (P_W). Les pentes des deux régressions ne diffèrent pas significativement ($p = 0{,}55$); la relation obtenue indique qu'une population de reproducteurs composée d'un nombre égal de truites sauvages et de truites de pisciculture produirait 63 % moins de recrues par reproducteur qu'une population composée entièrement de poissons sauvages. Les résultats de l'étude ne sont pas affectés par les niveaux probables des erreurs de données, ni par les corrélations accessoires entre l'habitat et P_W. Les évaluations du statut des populations et les efforts de surveillance des activités de conservation devraient donc utiliser P_W comme variable critique. Le retrait, plutôt que l'addition, de poissons de pisciculture est peut-être la stratégie la plus efficace pour augmenter la productivité et la résilience des populations naturelles.

[Traduit par la Rédaction]

Introduction

Throughout the native range of anadromous salmonids, fish hatcheries are operated to enhance fisheries and, in some cases, to provide additional adults to supplement natural spawning populations in areas where wild fish are in low abundance. Therefore, either by design or by unintentional consequence, adult hatchery fish spawn naturally in many streams occupied by wild fish. In recent years, the impact of such naturally spawning hatchery fish has become an issue of considerable interest with respect to their impact on the biological health of wild populations (Waples 1991; Busack and Currens 1995; Campton 1995). In the United States, as the number of wild salmonid populations placed under the protection of the Endangered Species Act have increased, so have the concerns regarding the impact of hatchery programs on wild fish (Sterne 1995).

Evidence from a number of studies (e.g., Nickelson et al. 1986; Leider et al. 1990; Reisenbichler and Rubin 1999) suggests that hatchery-reared fish may be less fit than wild fish under natural spawning and stream-rearing conditions. It is not clear if such results are the reflection of a relatively common phenomenon or if they represent the exceptions to a general condition of reproductive similarity between wild and hatchery fish.

In this study, measures of population productivity were used to indirectly examine the possibility of differential reproductive success between wild and hatchery fish in 12 populations of steelhead (*Oncorhynchus mykiss*). This examination was based on the assumption that if reproductive differences exist, productivity should vary in relation to the relative frequency of wild and hatchery fish in the spawning

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population. For example, if differences exist, it would be expected that natural populations consisting entirely of wild fish would be more productive, in terms of recruits produced per spawner, than those consisting of both hatchery and wild fish. The issue of population productivity also plays a central role in the development of species status assessments and conservation strategies. Understanding how various factors may influence population productivity is an important dimension of such conservation efforts. Therefore, the objectives of this study were twofold: first, to look for indirect evidence of reproductive differences between wild and hatchery fish and, second, to assess the influence of naturally spawning hatchery fish on overall population productivity.

Materials and methods

Populations and estimation of abundance

Only those populations for which spawner abundance data were available for a time period of at least 15 years were selected for use in this study. Of the 19 steelhead populations within the State of Oregon that met this selection criterion, seven were excluded from the study because of previously known data shortcomings with respect to the reliability of estimates for annual fish abundance and (or) the relative frequency of wild and hatchery origin spawners. The 12 populations selected for study were from a variety of different-sized watersheds and distributed widely across Oregon (Fig. 1). These included eight summer-run (SR) populations designated RogueSR, N.UmpquaSR, Deschutes, Upper John Day, Umatilla, Joseph, Camp, and Little Sheep and four winter-run (WR) populations designated RogueWR, N.UmpquaWR, Clackamas, and S.Santiam (Fig. 1). Summer-run refers to the race of steelhead that returns to freshwater during the summer and fall months and spawns the following spring. Winter-run refers to the race of steelhead that returns during the late winter and spawns shortly thereafter in the spring of the same year.

For 9 of the 12 populations, annual counts of steelhead as they passed a dam or fish ladder were used to derive spawner abundance estimates. Spawner abundance estimates for populations in the upper John Day River, Joseph Creek, and Camp Creek, which lack fish-counting facilities, were derived from redd counts obtained for a subset of the spawning habitat. For most populations, annual estimates of spawner escapement were obtained for the period from 1974 to 2002. However, for the Deschutes and Little Sheep populations, the data periods began in 1978 and 1985, respectively. The annual frequencies of wild fish for most populations were determined from the classification of returning adults as either hatchery or wild fish based on fin mark observations. Fish missing a fin were presumed to be hatchery fish because adipose fins were excised from hatchery steelhead before their release as smolts. Fish without missing fins were assumed to be wild fish. Hatchery steelhead smolts were not released into basins occupied by the Upper John Day, Joseph, and Camp populations. However, hatchery fish from out-of-basin programs may have strayed into these populations and spawned. Detection of such strays was problematical because only a small fraction of the total spawners were observable during spawning surveys. However, from this limited sample, the observed absence or presence of fin clip marks on individual fish (both dead and alive) were used to estimate the frequency of wild and hatchery fish in the spawning population. Additional details concerning the methodologies used to determine spawner abundance and frequency of wild fish follow.

The RogueSR and RogueWR populations, located in the upper Rogue River basin, were counted at Gold Ray Dam as they passed a fish ladder viewing window. Counts were made directly by an observer or indirectly from video-camera recordings. Most hatchery fish subsequently returned to Cole M. Rivers Hatchery and were removed from the natural spawning population. Cole M. Rivers Hatchery is located 52 river km upstream from Gold Ray Dam. Similar procedures were used for the N.UmpquaSR and N.UmpquaWR populations at the Winchester Dam fish-counting facility, located near the mouth of the North Umpqua River. Similar methodology was also used at the North Fork Dam located in the lower portion of the Clackamas River to count the Clackamas population. However, before 1995, hatchery fish returning to the Clackamas basin were not fin-clipped. For this earlier time period, hatchery fish and wild fish were identified on the basis of known differences in run timing. Fish returning before 1 April were classified as hatchery fish, and those returning after 1 April were classified as wild fish. The use of 1 April as the date to separate hatchery and wild fish was based on run-timing observations made after 1995 when all hatchery fish were fin-marked. In this post-1995 time period, it was found that the run-timing method yielded wild fish abundance estimates that differed by less than 5% from those based on the fin-clip observation methodology. The S.Santiam population was counted and hatchery–wild classifications were made by examination of individual fish captured in a trap at Foster Dam, located on the South Santiam River.

The Deschutes population reproduces in that portion of the Deschutes River basin accessible to anadromous fish upstream from Sherars Falls. Sherars Falls is an impediment to upstream fish migration, but not a barrier. Although a ladder exists at Sherars Falls to facilitate migration, many fish negotiate the falls directly and do not use the ladder. Mark–recapture methodologies were used to estimate the total number of fish that migrated past Sherars Falls. Fish captured in the Sherars Falls ladder were marked with anchor tags and passed upstream. The recapture and count of marked and unmarked steelhead were made at traps located upstream at Pelton Dam and Warm Springs National Fish Hatchery.

Estimation of escapement for the Deschutes population was complicated by the high incidence of stray steelhead originating from hatcheries located in Idaho and northeast Oregon (Olson et al. 1995). These strays were identified as such because the hatchery fish released into the Deschutes basin bore unique fin-clip marks and therefore could be distinguished from out-of-basin strays. It was assumed that a substantial portion of these stray hatchery fish left the Deschutes basin before spawning and returned to their natal streams. To account for this behavior, the mark–recapture estimate for stray hatchery spawners was adjusted downward by 50%. The rationale for this adjustment was based on the recovery of fish at hatcheries outside of the Deschutes River

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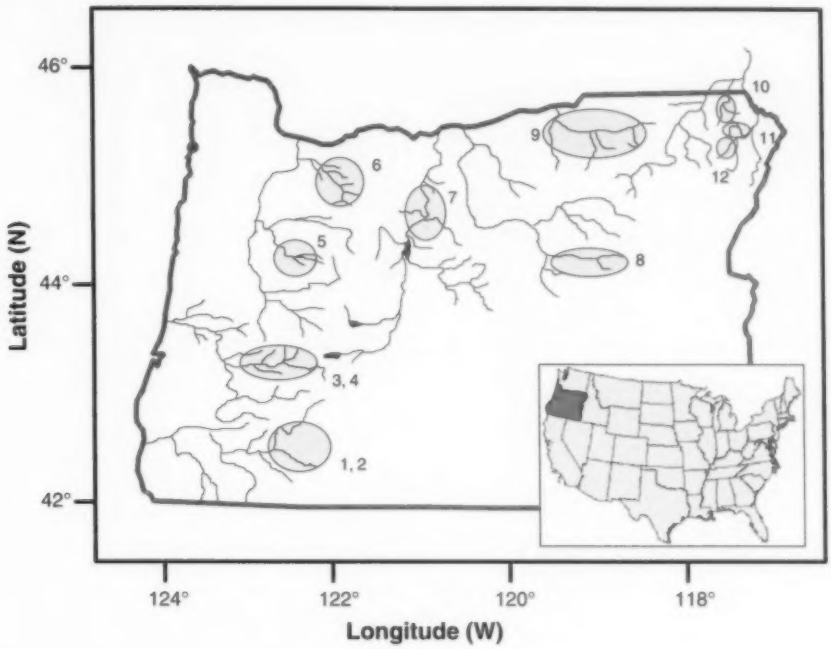
Fig. 1. Location within the state of Oregon, U.S.A., of 12 populations of steelhead (*Oncorhynchus mykiss*) used to evaluate the relationship between population productivity and proportion of wild fish in spawning population. 1, RogueSR; 2, RogueWR; 3, N.UmpquaSR; 4, N.UmpquaWR; 5, S.Santiam; 6, Clackamas; 7, Deschutes; 8, Upper John Day; 9, Umatilla; 10, Joseph; 11, Camp; 12, Little Sheep.



basin bearing anchor tags that had been applied at Sherars Falls earlier in the migration season. Additional evidence for this behavior were data from a radio-tagging study that indicated at least 50% of the radio-tagged fish that passed Sherars Falls were subsequently detected exiting the Deschutes River (Steve Pribyl, Oregon Department of Fish and Wildlife District Office, 3701 West 13th, The Dalles, OR 97058, personal communication).

The Upper John Day population reproduces in the mainstem John Day River basin upstream from the mouth of the South Fork John Day River. Of the 688 linear km of stream habitat in the Upper John Day basin, 43 km were surveyed to annually count steelhead redds. From redd count data, the average redd density for the survey sections was calculated and applied to the total stream km in the basin to obtain an estimate of total redds. This total redd estimate was converted to total spawner abundance using the approach described by the Oregon Department of Fish and Wildlife (ODFW; 2001), wherein each completed redd was assumed to represent 0.8 females and 40% of the spawning population was assumed to be male. The Umatilla population was counted at Threemile Dam, located near the mouth of the Umatilla River. Since 1988, all steelhead trapped at Threemile Dam were individually classified as either wild or hatchery fish and passed upstream. Before 1988, the fish trap was not operated continuously throughout each day. Trap catch rates for returning adults were used to estimate the number of fish that passed uncounted during periods when the trap was not fished.

The Joseph population occurs in a major tributary to the lower Grande Ronde River, Joseph Creek. Of the 354 total linear stream km occupied by this population, 69 km were surveyed annually for steelhead redds. The Camp population is located in Camp Creek, a subbasin within the Imnaha River watershed. Eight of the total 33 linear stream km occupied by this population were surveyed annually for steelhead redds. For both the Joseph and Camp populations, the conversion of redd survey data to total fish was the same as described previously for the Upper John Day population. The Little Sheep population is also located within the Imnaha River basin. Fish were trapped at a permanent counting weir near the mouth of Little Sheep Creek and individually counted as hatchery or wild fish.

Age composition of wild fish

For most populations, the age composition of returning adult steelhead was determined from age analysis of scales sampled from steelhead caught in sport fisheries. However, for the Little Sheep population, scales for age analysis were obtained from fish trapped at the counting weir. In addition, no scale samples were available for fish returning to the Joseph and Camp populations. Because population-specific data were lacking, it was assumed that the age composition of these two populations was the same as the most proximate population, Little Sheep. For most populations, age data were rarely available for a period of more than 10 years. Because of this limitation, age-composition data for all years were pooled and an average age composition

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was calculated for each population. This age information was used with abundance estimates for individual return years to approximate the number of adults of each age.

Fishery catch and mortality rates

Population-specific estimates of fish mortality resulting from recreational fisheries were based on unpublished estimates of catch rates from a variety of studies conducted by the Oregon Department of Fish and Wildlife (Kenaston 1989). In these studies, catch estimates were developed from a stratified sampling of total fishery effort (number of angler-days) and angler success rates (fish per angler-day as determined from interviews of a subset of the anglers). By coupling these numbers with escapement estimates, it was possible to estimate the fraction of the population that was caught (catch rate). Because the number of annual catch estimates for each population was typically limited to less than five, an average catch rate was calculated and used to represent recreational-fishery catch rate for each population (Table 1). Direct estimates of catch rate for Upper John Day, Umatilla, Joseph, Camp, and Little Sheep populations were not available. Because most of these populations are located in relatively remote areas of Oregon, it was assumed that the intensity of the associated fishery was low. In the absence of specific information, a default catch rate of 0.11 was suggested by Kenaston (1989) for low-intensity summer-run steelhead fisheries. This default (0.11) was used as catch rate for Upper John Day, Umatilla, Joseph, Camp, and Little Sheep populations.

In general, the fish mortality rate resulting from recreational fisheries was assumed to be the same as the catch rate. However, between 1978 and 2001, depending on the location, fishing regulations were implemented to reduce mortalities on wild steelhead. In most cases, these regulations required that all wild fish caught had to be released (only hatchery fish could be kept). It was assumed that the post-release handling mortality of these caught and released steelhead was 10%. Therefore, the effective mortality rate of fisheries after implementation of these regulations was 0.10 of the catch rate. In addition to recreational fisheries, Columbia basin steelhead populations from the Deschutes eastward were impacted by a commercial gillnet fishery in the mainstem Columbia River. From 1985 to present, annual commercial fishery mortality rates on wild steelhead were assumed to be the same as those published by ODFW and Washington Department of Fish and Wildlife (WDFW; 2001). Commercial-fishery impact rates from 1974 to 1984 were estimated as the average of annual rates observed from 1985 to 1990. The combined impact of both recreational and commercial fisheries on each year's return of each population was estimated from

$$(1) \qquad F = 1 - [(1 - F_c)(1 - F_r)]$$

where F is the combined fishery mortality rate for wild fish, F_c is the mortality rate from commercial fisheries, and F_r is the mortality rate from recreational fisheries.

Escapement and recruitment

Annual counts of returning fish were converted into estimates of annual spawning escapement from

Table 1. Assumed recreational-fishery catch rates for 12 populations of Oregon steelhead partitioned for fisheries downstream and upstream of adult return counting location.

Population	Downstream	Upstream	Cumulative[a]
RogueSR	0.11	0.11	0.21
RogueWR	0.08	0.08	0.15
N.UmpquaSR	0.11	0.39	0.46
N.UmpquaWR	0.13	0.08	0.20
Clackamas	0.34	0.12	0.41
S.Santiam	0.13	0.08 (0.00)[b]	0.20 (0.13)
Deschutes	0.19	0.11	0.28
John Day	0.11	No fishery	0.11
Umatilla	0.01	0.10	0.11
Joseph	0.11	No fishery	0.11
Camp	0.11	No fishery	0.11
Little Sheep	0.11	No fishery	0.11

[a]Cumulative catch rate = 1 – [(1 – downstream rate) × (1 – upstream rate)].

[b]Upstream catch rate = 0.00 from 1994 to 2002 because steelhead fishery was closed.

$$(2) \qquad S_w = \mathrm{Count}_w(1 - \mathrm{Fup}_w) - \mathrm{Remov}_w$$

$$(3) \qquad S_h = \mathrm{Count}_h(1 - \mathrm{Fup}_h) - \mathrm{Remov}_h$$

where S_w and S_h are spawner escapement estimate for wild or hatchery fish, respectively; Count_w and Count_h are basin count of wild or hatchery fish, respectively; Fup_w and Fup_h are estimated fishery mortality rate for wild and hatchery fish upstream from counting location, respectively; and Remov_w and Remov_h are number of wild and hatchery fish removed at basin hatcheries, respectively. The average proportion of wild fish in the spawning population (P_w) was calculated as

$$(4) \qquad P_w = (1/n)\sum[S_{w_t}/(S_{w_t} + S_{h_t})]$$

where S_{w_t} and S_{h_t} represent the number of spawners for brood year t for wild and hatchery fish, respectively. The number of natural recruits (wild fish) produced by each brood year of spawners was estimated from

$$(5) \qquad R_t = \sum_{j=2}^{8}[(A_j S_{t+j})/(1 - F_{t+j})]$$

where R_t represents the number of wild recruits produced by fish that spawned in year t, A_j is the proportion of fish having age j at spawning (j = 2, 3, 4, 5, 6, 7, and 8), S_{t+j} is the number of wild spawners in year $t + j$, and F_{t+j} is the fishing mortality rate for the return of fish that spawned in year $t + j$.

Mean productivity (G_m) was calculated for each population as

$$(6) \qquad G_m = (1/n)\sum \ln(R_t/S_t)$$

where S_t is the total number of wild plus hatchery fish that spawned in year t, and R_t is the number of wild recruits produced by S_t spawners. A second index of productivity, intrinsic productivity (G_i), was estimated by fitting the Ricker recruitment model (eq. 7) to data for each population and using the value obtained for the equation parameter a to represent G_i as follows:

$$(7) \qquad R = Se^{(a-BS)}$$

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Table 2. Estimated average proportion of wild fish in spawning population (P_w), index of hatchery broodstock suitability (Suitability), proportion of basin with consolidated geology (Geology), basin road density (Roads; expressed as road km/km^2 of basin area), and number of large dams in migration corridor (Dams) for 12 populations of Oregon steelhead and their associated habitats.

Population	P_w	Suitability	Geology	Roads	Dams
RogueSR	0.852	4.0	0.60	2.69	0
RogueWR	0.936	5.0	0.60	2.69	0
N.UmpquaSR	0.493	6.0	0.44	1.89	0
N.UmpquaWR	0.928	1.0	0.44	1.89	0
Clackamas	0.796	1.0	0.40	1.72	1
S.Santiam	0.835	3.0	0.27	2.40	1
Deschutes	0.516	4.3	0.65	1.22	2
Upper John Day	0.994	3.0	0.66	1.34	3
Umatilla	0.897	7.0	0.16	2.32	4
Joseph	1.000	—[a]	0.08	1.73	8
Camp	1.000	—[a]	0.07	1.53	8
Little Sheep	0.384	6.0	0.08	2.34	8

[a]Index value omitted because no hatchery fish mixing with this population.

(8) $G_i = a$

where R represents wild recruits and S represents total spawners (wild plus hatchery fish). Ricker recruitment equation parameters a and B were estimated using both the linear least squares and the nonlinear maximum likelihood methods.

Regression analyses

To examine the relationship between productivity and the frequency of wild fish in the spawning population, regressions of G_m and G_i on P_w for the 12 population data set were performed. Possible relationships between P_w and other factors thought to influence productivity, such as variations in habitat quality and hatchery broodstock suitability for natural production, were also examined. To accomplish this, regression analyses were performed between P_w and indices for (*i*) the suitability of the hatchery broodstock for natural reproduction, (*ii*) the innate quality of the stream habitat, (*iii*) the extent of human impact on stream habitats, and (*iv*) the extent to which steelhead migration corridors between the freshwater and marine environments had been adversely effected by human-caused changes.

The index for hatchery broodstock suitability was devised to quantify assumed differences among the various kinds of hatchery fish in terms of their ability to successfully reproduce under natural conditions. This index was calculated by summing the individual scores for five broodstock-suitability attributes. The scoring criteria for each attribute were as follows: attribute 1 (broodstock source), score = 0 if source is from different evolutionarily significant unit (ESU), based on ESU boundary descriptions of Busby et al. (1996), score = 1 if source is from same ESU, and score = 2 if source is from same wild population; attribute 2 (mean proportion of local wild fish used in hatchery broodstock), score = 0 if proportion of wild fish is <0.10, score = 2 if proportion of wild fish is 0.10 to 0.50, and score = 3 if proportion of wild fish is >0.50; attribute 3 (mean age of hatchery broodstock during period of study), score = 0 if older than 20 years, score = 1 if 10 to 20 years old, and score = 2 if less than 10 years old; attribute 4 (spawn timing relative to wild fish), score = 0 if hatchery fish spawn earlier than wild fish, score = 1 if hatchery and wild fish spawn at similar times; attribute 5 (age of hatchery smolts), score = 0 if age of hatchery smolts is younger than wild smolts, score = 1 if at least 50% of the hatchery smolts are of the same age as wild smolts.

The proportion of a basin having consolidated, nonerosive geology was used as an index of innate stream habitat quality. To estimate values for this index, a geologic overlay map for each basin was used to classify the underlying rock formation as either consolidated (e.g., basaltic) or unconsolidated (e.g., sedimentary). Road density, expressed as linear km of roads/basin km^2, was used as an index of human impact on stream habitat. Total mileage of paved and unpaved roads within a basin, as determined from geographic information system (GIS) overlays, was divided by total basin area to calculate this index. The index for human-caused changes in the steelhead migration corridor was a simple count of dams higher than 15 m that members of each population had to negotiate as smolts and adults going to and from the ocean.

Sensitivity analysis

An analysis was performed to assess the impact of potential errors related to data measurement, approximation, and assumption. The simulated outcome of regressing productivity on P_w was used as the standard for evaluating these errors. The key data elements considered in this analysis were total spawner abundance (S_{tot}), abundance of wild spawners (S_w), fishery mortality on wild fish (F_w), and the age composition of wild fish expressed as the number of fish at each age (A_{wj}, for j = 2 to 8). A summary of the algorithm that directed this simulation follows.

Step 1: For each population, enter annual measured values for the number of naturally spawning hatchery and wild fish, fishery mortalities, and age composition.

Step 2: For each population, enter a model run coefficient of variation ($CV_i = \sigma/x$) for $i = S_{tot}$, S_w, F_w, and A_{wj}.

Step 3: Obtain random numbers (N_{ran}) from a normal distribution having a mean of 0 and variance of 1.

Step 4: For each year of data, adjust total number of spawners (wild plus hatchery fish) such that $SA_{tot} = S_{tot} + (S_{tot})(CV_{S_{tot}})(N_{ran})$.

Step 5: For each year of data, compute the adjusted number of wild spawners from $SA_{S_w} = SA_{S_{tot}}(P_w) + (SA_{S_{tot}})(P_w)(CV_{S_w})(N_{ran})$, where P_w is the proportion of wild fish observed in spawning population and N_{ran} is a new random number.

Step 6: For each year, compute the adjusted number of fishery mortalities for wild fish from $FA_w = F_w + (F_w)(CV_{F_w})(N_{ran})$, where $F_w = [SA_{S_w}/(1 - F_w)] - SA_{S_w}$, N_{ran} is a new random number, and F_w is the observed fishing mortality rate on wild fish.

Step 7: For each return of wild fish, compute the prefishery abundance for each age group from $A_{wj} = Age_j(Ab) + Age_j(Ab)(CV_{A_{wj}})(N_{ran\,j})$, where j = age from 2 to 8 years old, Age_j is the estimated mean proportion of age-j fish in returning population, $Ab = SA_{S_w} + FA_w$, and $N_{ran\,j}$ is a new random number for each j.

Step 8: Repeat steps 3 to 7 for all years of data set.

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Table 3. Estimated proportion of different-aged fish at time of spawning for 12 populations of Oregon steelhead.

	Age at time of spawning							
Population	2	3	4	5	6	7	8	*n*
RogueSR	0.000	0.049	0.610	0.268	0.049	0.024	0.000	41
RogueWR	0.036	0.212	0.468	0.270	0.014	0.028	0.000	222
N.UmpquaSR	0.000	0.035	0.175	0.474	0.298	0.018	0.000	57
N.UmpquaWR	0.000	0.142	0.356	0.351	0.134	0.013	0.004	239
Clackamas	0.007	0.113	0.472	0.324	0.085	0.000	0.000	142
S.Santiam	0.000	0.195	0.488	0.268	0.024	0.024	0.000	41
Deschutes	0.000	0.500	0.250	0.200	0.050	0.000	0.000	20
Upper John Day	0.000	0.376	0.324	0.256	0.044	0.000	0.000	250
Umatilla	0.000	0.044	0.294	0.563	0.100	0.000	0.000	160
Joseph, Camp, Little Sheep[a]	0.000	0.011	0.700	0.261	0.028	0.000	0.000	263

Note: *n* = number of fish that were aged for each population.

[a]Scale samples were collected only from Little Sheep steelhead and were assumed to be representative of steelhead belonging to the Joseph and Camp populations.

Table 4. Ricker recruitment model parameters *a* and *B* (expressed as 1/*B*) estimated using linear and nonlinear methodologies for 12 populations of Oregon steelhead.

		Linear				Nonlinear	
Population	*n*	*a*	1/*B*	R^2	*p*	*a*	1/*B*
RogueSR	23	1.268	5132	0.53	0.00	1.268	5132
RogueWR	23	1.619	4736	0.85	0.00	1.617	4743
N.UmpquaSR	23	0.936	6210	0.72	0.00	0.936	6210
N.UmpquaWR	23	1.309	5542	0.74	0.00	1.309	5544
Clackamas	23	0.651	1872	0.11	0.12	0.651	1872
S. Santiam	23	0.718	568	0.72	0.00	0.718	568
Deschutes	23	0.349	9903	0.29	0.02	0.349	9905
Upper John Day	19	1.153	4161	0.48	0.00	1.153	4161
Umatilla	23	1.423	1414	0.53	0.00	1.422	1415
Joseph	23	1.414	1186	0.51	0.00	1.414	1186
Camp	23	1.486	140	0.56	0.00	1.486	140
Little Sheep	12	–0.034	255	0.68	0.00	–0.034	255

Step 9: For each brood year of spawners, estimate the number recruits using the following equation:

$$(9) \qquad R_t = \sum_{j=2}^{8} A_{w_{t+j}}$$

Step 10: Compute the average proportion of wild fish in the spawning population using the equation

$$(10) \qquad P_w = (1/n) \sum (SA_{S_w} / SA_{S_{tot}})$$

Step 11: Use least squares method to estimate the Ricker recruitment model parameter *a* for the population.

Step 12: Repeat steps 3 to 11 for each population.

Step 13: Using data from all populations, regress G_i (i.e., Ricker *a* parameter) on P_w, determine significance probability and slope of the linear regression, and store result.

Step 14: Repeat 500 times steps 3–13.

Step 15: Determine the number of iterations out of 500 that yielded a regression with a positive slope that was statistically significant ($p \leq 0.05$).

Results

The estimated proportion of wild fish in each spawning population (P_w) ranged from 0.384 to 1.000 (Table 2). For the Upper John Day, Joseph, and Camp populations, the total number of fish examined to estimate the frequency of wild spawners was 466, 30, and 29, respectively. These numbers represent a small fraction of the estimated spawning abundance for these populations, a consequence of not being able to sample fish at counting facilities, as was the case for the other nine populations. A compilation of age data indicated the most common adult ages were 3, 4, and 5 (Table 3). Five or more age classes were found in steelhead populations occurring in western Oregon, whereas populations occurring in central and eastern Oregon had four or fewer age classes.

Productivity estimates for each population were based on the observed relationship between spawners and subsequent recruits. As illustrated in Fig. 2, the Ricker recruitment model fit population data with varying degrees of success. The R^2 values associated with the linear estimation of recruitment equation parameters ranged from 0.11 to 0.85 depending on the population (Table 4). Linear and nonlinear parameter estimation methodologies yielded essentially equal population

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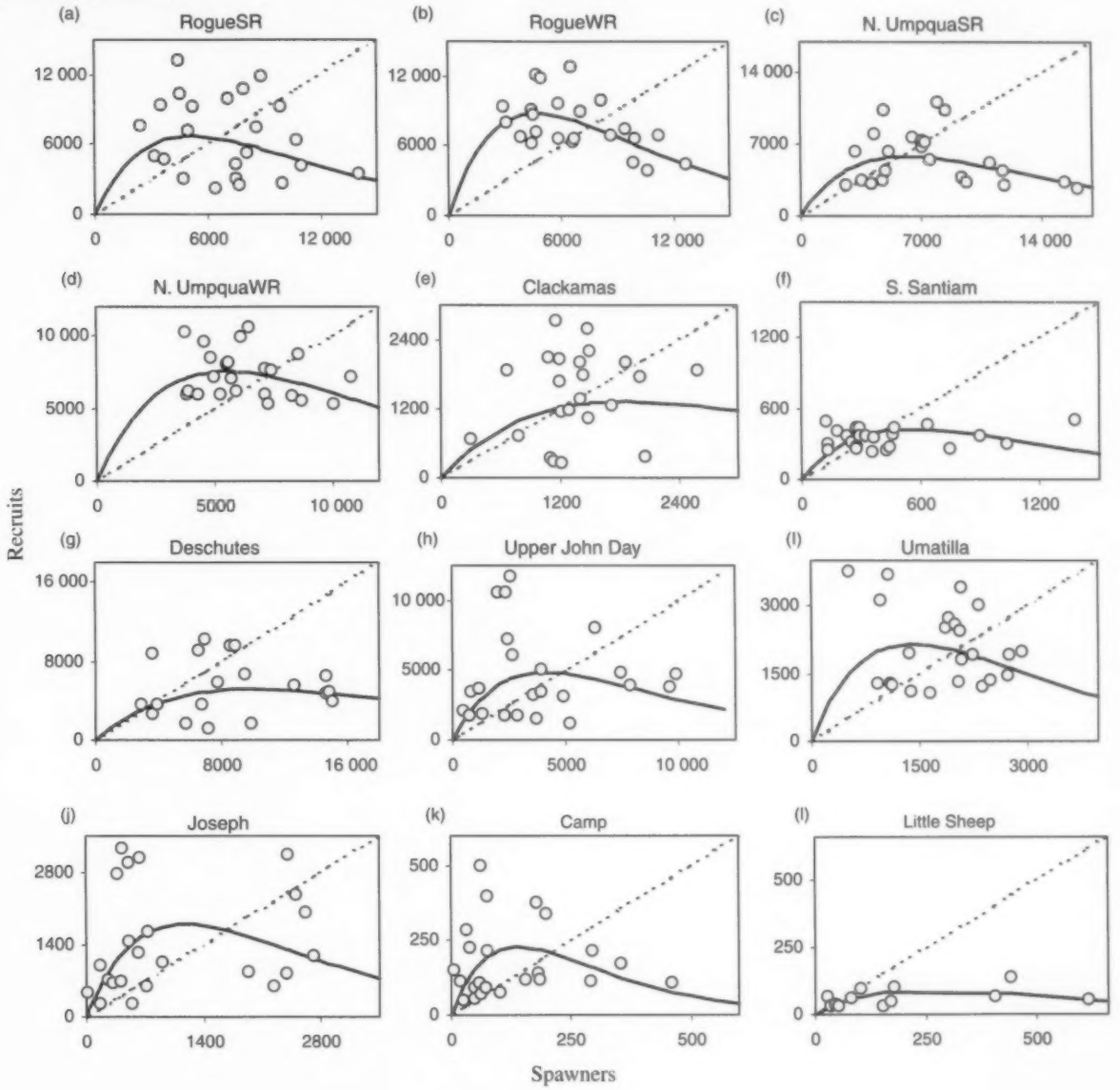
Fig. 2. Relationship between spawners and subsequent recruits for 12 populations of Oregon steelhead (*Oncorhynchus mykiss*), 1974 to 1996 brood years. Solid line represents curve for Ricker recruitment model fit to each data set; broken diagonal line indicates recruits = spawners (replacement).



estimates for the Ricker equation parameters a and B (Table 4). A regression of G_m on the average proportion of wild fish in the spawning population (P_w) yielded a statistically significant positive relationship ($p < 0.001$), having an R^2 of 0.88, a slope of 1.70, and an intercept of –1.37 (Fig. 3). A parallel result was obtained from the regression of G_i on P_w, which yielded a significant regression ($p < 0.001$) having a R^2 of 0.70, a slope of 1.97, and an intercept of –0.56. Although the elevations of these two regressions were statistically different ($p < 0.001$), the slopes were not ($p > 0.50$). A dispersed range of values characterized population indices for hatchery broodstock suitability, basin geology, and dams (Table 2). Less variability was observed with respect to values for road density. The significance probability for regressions of hatchery suitability, basin geology, roads, and dams indices on P_w was 0.22, 0.94, 0.99, and 0.93, respectively.

From simulation modeling, it appeared that the probability of obtaining a significant regression ($p < 0.005$) of G_i on P_w was sensitive to error associated with S_w (number of wild spawners) and S_{tot} (total spawners). For example, increasing the CV from 0.10 to 0.60 for S_w, decreased the probability of obtaining a significant regression from 1.00 to 0.41

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Fig. 3. Relationship between the proportion of wild fish in the spawning population (P_w) and two measures of productivity (intrinsic productivity (G_i; circles) and mean productivity (G_m; triangles)) for 12 naturally reproducing steelhead (*Oncorhynchus mykiss*) populations in Oregon.

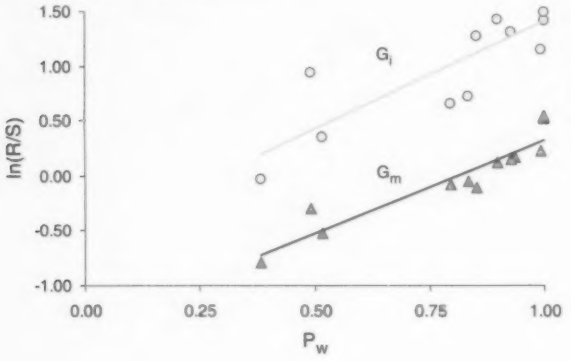
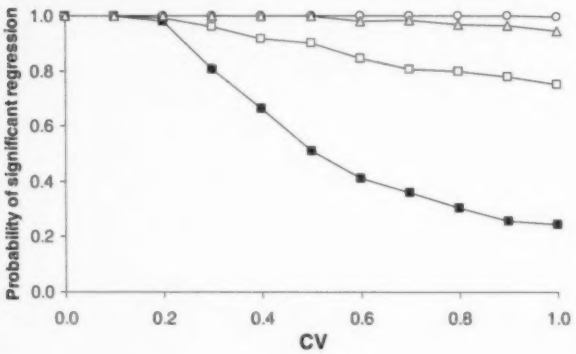


Fig. 4. The relationship between the coefficient of variation (CV) with respect to key data elements and the probability that the regression of productivity on proportion of wild spawners was statistically significant for model simulations involving data from 12 populations of Oregon steelhead (*Oncorhynchus mykiss*). Key data elements were fishing mortality on wild fish (○) and age composition of wild fish (△), total spawners (□), and wild spawners (■).



(Fig. 4). For S_{tot}, the same increase in CV (0.10 to 0.60) yielded a decrease in the frequency of significant regressions from 1.00 to only 0.81. In contrast, similar analyses for F_w (fishing-associated mortality) and A_{wj} (assumed age distribution) demonstrated that CV values as high as 1.0 had only minor effects on the regression outcomes of G_i on P_w (Fig. 4). A second stage of sensitivity analyses were performed wherein the most probable coefficients of variation for all key elements were analyzed together in the same model run. Based on the known details of the data collection methodologies and likely associated errors, a matrix of "best guess" CV values was developed for all populations and data elements (Table 5). When simulations were conducted using this best guess matrix, it was found that in 494 of 500 iterations (0.99), the regression of G_i on P_w was significant. Three additional error scenarios were simulated. In the first of these, for which CV values for S_{tot} and S_w were incremented by 0.20 over the best guess scenario, the probability of obtaining a significant regression was 0.94. In the next simulation, wherein CV values for all data elements were increased by an additional 0.20, the probability of obtaining a significant regression was reduced to 0.83. Lastly, when CV values were incremented yet another 0.20, the probability of a significant regression was 0.75.

Table 5. "Best guess" estimates of coefficients of variation for key data elements, total spawners (S_{tot}), wild spawners (S_w), fishing mortality on wild fish (F_w), and age composition of wild fish (A_w), as used to evaluate the relationship between population productivity and proportion of spawners that were wild fish for 12 populations of Oregon steelhead.

Population	S_{tot}	S_w	F_w	A_w
RogueSR	0.20	0.20	0.40	0.60
RogueWR	0.20	0.20	0.40	0.60
N.UmpquaSR	0.20	0.20	0.40	0.60
N.UmpquaWR	0.20	0.20	0.40	0.60
Clackamas	0.20	0.20	0.40	0.60
S.Santiam	0.00	0.00	0.40	0.60
Deschutes	0.40	0.40	0.60	0.60
Upper John Day	0.40	0.40	0.60	0.60
Umatilla	0.00	0.00	0.60	0.60
Joseph	0.40	0.40	0.20	0.60
Camp	0.40	0.40	0.20	0.60
Little Sheep	0.00	0.00	0.20	0.60

Discussion

Study results suggest that a relationship existed between population productivity and the average proportion of wild fish in the spawning population. Those steelhead populations with a high frequency of wild fish tended to be more productive than those with a lower frequency of wild fish (more hatchery fish). The apparent magnitude of this effect was substantial. For example, a P_w value of 1.00 substituted into the intrinsic productivity regression equation yielded a G_i of 1.414, whereas a P_w value of 0.50 yielded a G_i value of 0.427. Arithmetically transformed, this represents a 63% loss in recruits per spawner as a consequence of a 0.50 decrease in P_w. A similar reduction in P_w when applied to the regression equation for G_m on P_w yields an arithmetically transformed reduction in recruits per spawner of 57%. The reliability of these findings is dependent on the correctness of several underlying assumptions related to the study's analytical framework and the quality of associated data. These included the selection of appropriate metrics to measure population productivity, the consideration of other habitat-related factors that could have confounded the relationship between productivity and P_w, and sensitivity to errors in the measurement of key data elements.

The relationship between spawners and subsequent recruits was the basis for measuring productivity. In populations that are habitat-limited, the relation between spawners and recruits varies with the density of spawners. The *a* parameter of Ricker recruitment model, represented in this study by G_i, provided a measurement of recruits per spawner standardized to a spawner abundance of near zero. Therefore, G_i, as

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a measure of productivity, had the desirable characteristic of being standardized for spawner density. However the weakness of this approach was that near-zero spawner abundance data are usually lacking and therefore the estimate of a must rely on model interpolation from data points often associated with moderate to high levels of spawner abundance. This situation existed for some of the populations of this study, as illustrated. In addition, poor fits of the data to the assumed recruitment model, as was the case for several populations evaluated in this study, further weakens the reliability of the interpolation necessary to estimate a. Although the linear parameter estimation method yielded relatively high R^2 values, the interpretation of these values was difficult because the linear estimation method tends to generate artificial relationships owing to the inherent problem of the independent variable, S, being included in the calculation of the dependent variable, $\ln(R/S)$. However, even though the fit of the data to the Ricker recruitment model was questionable for several populations, linear and nonlinear parameter estimates of a were essentially the same.

The other measure of productivity used in this study, G_m, had the methodological advantage of being calculated directly from observed spawner and recruit data without the overlay of an assumed recruitment model or interpolation into zones without data. However, G_m was not standardized for any possible effect of density dependence, potentially a significant problem if productivity was less when the density of spawners was high and if high spawner density and high incidence of hatchery fish (low P_w) were correlated. Because it is difficult to judge how the populations compared in terms of spawner densities relative to habitat capacity, an evaluation of this problem was not possible, and therefore its significance is unknown.

Although the estimation of both G_i and G_m had technical shortcomings, their relationship with P_w appeared similar in terms of the slopes of the two regression lines that were resolved. For any given change in P_w, the relative responses of G_i and G_m were statistically inseparable. Similar results from these two dissimilar measures of productivity added weight to the likelihood that the productivity of naturally reproducing populations of steelhead was linked to the frequency of wild spawners in the population. However, there were other factors that may also have influenced productivity, in particular, among population differences in habitat quality and differences in the natural reproductive performance of various hatchery broodstocks. As part of the formula for obtaining an unambiguous evaluation of the relationship of P_w and population productivity, it was important to confirm the independence of P_w from these other, potentially confounding factors. For example, suppose basins with relatively healthy habitat and wild populations were less frequently selected for hatchery programs than were basins with poor habitat and depressed productivity of the wild population. In such a case, it would be erroneous to interpret an association between low P_w values (more hatchery fish) and low productivity as an effect of hatchery fish. Habitat differences would be the actual cause behind the observed association. However, evidence of such problems was not found. The analysis failed to demonstrate any relation between P_w and intrinsic habitat quality as indexed by the proportion of consolidated basin geology, as well as by human-caused habitat degradation as indexed by road density. Further, variation in migration survival as indexed by the number of dams in the migration corridor did not appear related to the distribution of P_w among the populations.

The conclusion that P_w was indeed independent of habitat quality was tied to the assumption that the indices used to represent habitat quality at the basin level were reliable. Because much of the fishery research related to habitat has been focused at smaller scales than the basin level (Schlosser 1991), larger scale indices of habitat quality that have been empirically authenticated are relatively uncommon (Thompson and Lee 2000). However, the indices selected for use in this study focused on this larger scale and did have an empirical basis. For example, Thompson and Lee (2000) found a link between the proportion of unconsolidated geology within a basin and production of age-1+ steelhead. With respect to road density, a variety of studies have reported that basins with high road densities produce fewer anadromous salmonids than those with low road densities (Thompson and Lee 2000; Paulsen and Fisher 2001; Sharma and Hilborn 2001). Finally, the basis for the dam index comes from evidence presented by Raymond (1988) and Schaller et al. (1999) suggesting that life cycle survival for anadromous salmonids decreases as the number of large hydropower dams that must be negotiated on the way to and from the ocean increases.

Although these results are consistent with the supposition that hatchery steelhead were distributed across Oregon in a manner that was random with respect habitat quality, it is still possible that populations with poor performance as a result of some other factor were more likely to have been targeted for supplementation with hatchery fish than were populations with better performance. This uncertainty could have been largely avoided if the distribution of hatchery fish had been formally randomized among the populations at the beginning of the study. However, because of this study's retrospective nature, such a step was not possible. Regardless, it seems improbable that the allocation of hatchery programs was closely tied to a factor that was both cryptic and significant in its effect with respect to population productivity. Therefore, in light of this and the previous discussion concerning potential associations with habitat, it seems tenable that hatchery fish were distributed among the study populations in a de facto randomized pattern.

In addition to habitat quality, the suitability of hatchery broodstocks for natural production was considered. Although a wide range of hatchery broodstocks were represented in this study, their distribution appeared to be independent of P_w. However, as with the habitat-quality factors, the significance of this finding was tied to the reliability of the index used. Unlike the indices for habitat quality, direct authentication for this index was not possible. However, this index is comprised of elements (e.g., broodstock origin, broodstock age, infusion rate of wild fish, and phenotypic divergence) that are identified as potentially significant in studies that examine the process of genetic divergence between hatchery and wild fish (Waples 1999; Lynch and O'Hely 2001; Ford 2002). Therefore, the constituent elements of the index are not dependent on novel concepts raised for the first time here.

Study data were collected using a variety of methods and assumptions, a reality that almost certainly introduced error.

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In modeling the potential effect of these errors, it appeared that the relationship between G_i and P_w was relatively insensitive to errors in the measurement of fishery-related mortality and assumed age composition. The same was not true with respect to the other two key data elements, the total number of spawners and the number of wild spawners. In particular, the apparent relationship between G_i and P_w degenerated when the coefficient of error for the number of wild spawners was modeled at values greater than 0.30. However, the simulated probability of obtaining a positive regression of G_i on P_w was high (99%) when errors for all four data elements were set at best guess estimates with respect to CV values. Even when simulated errors were raised to improbable levels (4th error scenario), 75% of the model runs yielded a positive regression. Therefore, it appeared unlikely that data error and chance explained the observed relation between productivity and P_w.

Data for nearly all populations were collected for the same time period, 1974 to 2002. However, a notable exception was the Little Sheep population for which the time series started in 1985. It was possible that Little Sheep data may have distorted the study results because they were collected during a period when the ocean survival of steelhead may have been generally depressed. For example, Hare and Mantua (2000) suggested that a regime shift in North Pacific Ocean conditions likely occurred in 1989. Further, Ward (2000) found that steelhead recruitment for the 1987 to 1994 brood years was substantially lower than for the period from 1976 to 1986. However, when data series for all populations was restricted to the later time period (1985 to 2002), the regression of G_i on P_w and G_m on P_w were both statistically significant ($p < 0.005$). Furthermore, the slopes from these regressions (1.656 for G_i on P_w and 1.443 for G_m on P_w) were not significantly different ($p > 0.35$) from those obtained with the longer data series (1974 to 2002). Therefore, it appeared the temporal data inconsistency associated with the Little Sheep population was unlikely a substantial source of error.

The primary finding of this study was the apparent relationship between productivity and the proportion of wild fish in the spawning population. It is possible that this relationship was an outcome of naturally spawning hatchery fish having lower reproductive success than wild fish. Presumably, if hatchery fish had lower reproductive success, they would produce fewer recruits per spawner than wild fish. Therefore, adding hatchery fish to a natural spawning population would be expected to cause overall productivity, as defined in this study, to decline. Lower reproductive success for naturally spawning hatchery steelhead has been documented in several other studies (Chilcote et al. 1986; Leider et al. 1990; Reisenbichler and Rubin 1999). However, it is also possible that this study's primary finding was the product of adverse ecological interactions between hatchery and wild fish and not differential reproductive success. Hatchery programs, in some unknown manner, may have been ecologically detrimental to the survival and recruitment of wild fish. This would have had a depressing effect on overall population productivity. It was beyond the scope of this study, partially because of the retrospective nature of its analytical design, to resolve the question of ecological versus reproductive mechanisms with respect to the observed relationship between productivity and P_w. However, this question is clearly a topic that seems a fruitful direction for future empirical research.

It appears, at least for these populations, that among-population differences in productivity were influenced by the relative mixture of wild and hatchery fish in the spawning population. If one were to infer that this relationship holds for all salmonids, then the possible management implications are fourfold. First, in conducting conservation status assessments, interpretation of past recruitment performance must incorporate the depressing effect of naturally spawning hatchery fish. Second, it is critical that fish conservation monitoring and evaluation efforts track the relative frequency of wild and hatchery fish in natural spawning populations. Third, strategies that use hatchery fish to rebuild depressed wild populations may be counterproductive because they are likely to cause a loss in overall population productivity and thereby cancel the recruitment benefit from adding hatchery spawners to the population. Fourth, an effective method to increase the productivity of natural populations and associated conservation benefits may be to minimize the frequency of hatchery fish in natural spawning populations.

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Finding fish: grouping and catch-per-unit-effort in the Pacific hake (*Merluccius productus*) fishery

Lore M. Ruttan

Abstract: Numerous papers have documented the problems in estimating stock abundance using only catch-per-unit-effort (CPUE) data. In this paper, logbook data from the onshore processing sector of the Pacific hake (*Merluccius productus*) fishery in Oregon from 1992 to 1996 are used to analyze the effect of grouping on CPUE and on search time. Two groups are investigated: (*i*) simple daily aggregations of vessels on fishing grounds and (*ii*) yearly information-sharing groups. It is found that both groups are positively associated with CPUE; however, in 1995, this result may be the spurious result of more vessels being drawn into the fishery by good conditions. It is argued that in other years, fishers benefit from grouping by being able to find high-quality patches. Fishers in larger groups also experienced lower search times from 1993 to 1995. However, a pattern of declining effect of information-sharing groups from 1993 to 1996 suggests that fishers who were relatively new to this fishery became less reliant on information-sharing networks for finding patches of fish, although fishers in larger groups still may have benefitted by being able to find higher quality patches.

Résumé : De nombreuses études ont signalé les problèmes qu'il y a dans l'estimation de l'abondance d'un stock à partir des seules données de captures par unité d'effort de pêche (CPUE). Des données provenant de journaux de bord de l'industrie de transformation du merlu du Pacifique (*Merluccius productus*) sur la côte de l'Oregon de 1992 à 1996 nous ont servi à analyser les effets des regroupements des navires de pêche sur CPUE et le temps de recherche. Deux types de regroupements ont été considérés, de simples rassemblements quotidiens des navires sur les sites de pêche et des groupes qui partagent chaque année leurs renseignements. Il y a une relation positive entre les deux types de regroupements et CPUE; cependant en 1995, cette relation peut avoir été le résultat d'un accroissement du nombre de navires de pêche sur les sites à cause des conditions favorables. Les autres années, les pêcheurs ont bénéficié des regroupements, car ils ont pu trouver des rassemblements de poissons de haute qualité. Les pêcheurs dans les grands groupes ont aussi passé moins de temps à la recherche du poisson de 1993 à 1995. Cependant, les effets du partage des renseignements ont perdu de leur importance de 1993 à 1996. Il semble donc que des pêcheurs relativement novices dans cette pêche commerciale aient été moins dépendants des réseaux de partage des renseignements dans la recherche de rassemblements de poissons. Néanmoins, les pêcheurs appartenant à des groupes plus grands ont peut-être eu le bénéfice de trouver des rassemblements de poissons de plus haute qualité.

[Traduit par la Rédaction]

Introduction

Numerous papers have documented the problems in estimating stock abundance using catch-per-unit-effort (CPUE) data. In trying to relate real fishing effort (the instantaneous rate of fish mortality) to nominal fishing effort, (e.g., time spent fishing, length of net, etc.), most CPUE-based stock assessments assume a constant catchability coefficient (Rothschild 1977). In other words, the proportion of the locally available stock that is captured by a unit of effort is a constant. However, this may not in fact be the case (Rothschild 1977; Swain and Sinclair 1994). Following Hilborn's (1985) call to study the search behavior of fishers and to better understand fleet dynamics, a steadily increasing number of papers have been published questioning the underlying assumptions of CPUE-based stock assessment methods that are typically used when research survey data are not available.

Several aspects of fishers' behavior may distort the relationship between CPUE and actual abundance. This is particularly the case when factors besides abundance affect where fishers choose to fish and what to fish for. For example, in a multispecies fishery, changes in the relative prices paid for various species may lead fishers to switch the target of their activities regardless of relative abundance of the species targeted (Allen and McGlade 1986). Babcock and Pikitch (2000) argue that management tools such as trip limits also lead to changes in which species are targeted. Sampson (1991) has used a theoretical approach to argue that fuel and wage costs affect fishers' decisions on where to fish, and furthermore, when fishers are limited by hold size, CPUE can be a nonlinear function of abundance. Skippers may also have preferences for fishing in certain areas, preferences that are related to costs, familiarity with an area, or proximity to their home port. These preferences may be related in complicated ways to the fact that particular fishers are consistently able to catch more per unit of effort (Hilborn and Ledbetter 1979; Squires and Kirley 1999; but see Pálsson and Durrenberger (1982)). Significantly, such variation in skipper or vessel per-

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formance may also result in particularly good patches being underutilized and poorer patches being overutilized (Abrahams and Healey 1990). Attention to costs of fishing in different areas and to the problems of competition that occur when too many fishers are in one area may also distort the relation between CPUE and abundance if vessels compensate by switching location in an ideal free manner (Abrahams and Healy 1990; Rijnsdorp et al. 2000; Gillis and Frank 2001). In other words, with perfect information about the quality of various patches, some fishers may move to patches that are of poorer quality, or more costly to fish, but where they experience less interference competition. The result is constant CPUE across patches despite variation in underlying levels of abundance. Finally, fishers are constantly improving their ability to find fish. This can lead CPUE, as measured by catch per unit of time spent fishing, to remain constant even with declines in actual stock size. The problem is especially acute when resources are clumped (e.g., in the case of abalone, see Breen (1992)). Although many recent papers on fisher behavior have focused on the negative effects of aggregation on CPUE, there are some reports demonstrating a positive relationship between catch and group size (Campbell et al. 1993; Hancock et al. 1995; and for a limited range of group sizes, see Rijnsdorp et al. 2000).

Information sharing and, more generally, aggregation raise similar problems for CPUE-based stock assessments. In this paper, group size is defined in two ways: (*i*) by the number of vessels fishing in proximity to one another, hereafter referred to as aggregation size, and (*ii*) by the size of information-sharing groups. Over the course of a season, vessels may be observed fishing near each other more often than would be expected from a random distribution. The existence and size of such groups are inferred from these patterns.

Extrapolating from Clark and Mangel's models of animal foraging (Clark and Mangel 1984, 1986), it might be thought that information sharing can aid fishers by permitting them to increase the area searched and reduce the time spent finding fish while catching the same amount. In their model, the gross rate of return to a forager is

$$(1) \qquad f(n) = \frac{\theta C}{\theta\tau + 1/\lambda n} = \frac{C}{\tau + 1/\lambda \min(m, n)}$$

where C is the forager's gut capacity, n is group size, m is the number of "meals" in a patch of size B ($m = B/C$), and $\theta = \min(1, m/n)$. Here, we can think of C as the vessel hold capacity, or maximum catch measured in pounds (1 pound (lb.) = 0.455 kg) of fish. The denominator represents the total amount of time taken to fill the animal, or vessel, to capacity. It is broken into two parts: the first term, τ, is handling time, i.e., the time spent harvesting a patch of a given size, and the second term represents the total search time. Search paths are random, boats are assumed to search independently, and λ is a Poisson parameter interpreted as patches found per unit time. If fishers in groups benefit from a reduction in search time ($1/\lambda n$), we would expect a positive correlation with the inverse of group size.

In the model, increases in overall rate of return per trip as a result of information sharing are predicted to occur as long as foragers are limited in how much they can harvest at one time (i.e., they have a fixed hold size), prey are found in patches large enough and scarce enough that groups can find them more quickly, and such patches or schools can "satiate" more than one individual, or vessel in this case. Note that rate of return in the model is not equivalent to CPUE because the latter does not normally include search time. However, if measures of effort were to include search time, then catchability coefficients would not be expected to be constant across all group sizes and, in fact, should increase exponentially over some range of effort (Rothschild 1977).

Even when effort is measured in a more usual manner, catchability coefficients may not remain constant with increasing group size. This is not evident from examining the Clark and Mangel model, which permits patches to vary in quantity of prey, but not in density (or other aspects of quality pertinent to a fisher). This is understandable because the model was not developed to explain patterns of fishing or even to explain the behavior of human foragers, but rather it was developed as a general argument about information sharing among animals. If variation in prey density within patches is explicitly considered, it is evident that sharing information about the quality of patches, from either talking to or observing other fishers, should permit fishers to increase the amount caught per tow. Therefore, CPUE of vessels belonging to such groups may be higher than that of vessels fishing solitarily (Eales and Wilen 1986; Campbell et al.1993; Hancock et al. 1995), even if search time is not included in the measurement of effort and even if information is shared passively (Vignaux 1996). Thus, through either reduced search time or an ability to target only the best patches, sharing information may provide strong economic incentives for fishers to form such networks (Wilson 1990). If so, stock estimates based on these more traditional measures of CPUE may still overestimate abundance. If should be noted, however, that an alternative explanation for a positive relationship between CPUE and group size may be that more vessels target hake when conditions are good. In this paper, this possibility is investigated by examining the relationship between the CPUE and the number of vessels fishing for hake on a given day.

It is also conceivable that increasing group size may have a negative effect on CPUE. Increasing numbers of vessels in one area may depress CPUE relative to what a solitary individual could take, either because the presence of others depresses the amount of fish available in the patch or because of direct gear conflicts. However, as described above, if fishers take competition into account when choosing where to fish, CPUE may remain constant across group sizes. In essence, there may be an ideal free distribution (Fretwell and Lucas 1970) of vessels across patches. As one reviewer of this paper also notes, such a negative relationship between grouping and CPUE might also be the spurious result of less efficient vessels joining the fishery for unrelated reasons such as another fishery being closed.

Background to the fishery

Pacific hake (*Merluccius productus*), also known commercially as Pacific whiting, is a migratory species. Fish spawn in Southern California during the winter, and schools migrate every spring as far north as British Columbia, traveling along relatively well-defined depth contours (Methot and Dorn 1995). Although the province of British Columbia and

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the states of Washington and California all have hake fisheries, by far the largest amount is caught off the coast of Oregon using vessels equipped with mid-water trawls.

Until recently, many U.S. fishermen considered hake to be trash. Its "tender", i.e., mushy, flesh did not command very high prices in the U.S. market (Radtke 1995). Furthermore, some percentage of fish is infected by a myxozooan parasite, which induces rapid deterioration of the flesh once the fish is caught. Technological breakthroughs allowing hake to be processed into surimi have led to a greater interest in the fishery (surimi is in turn used to make imitation crab meat and other high-value fish products). As a consequence, foreign and joint venture fisheries that had operated on the West Coast since 1966 have been phased out and a wholly domestic fishery developed by 1991. Presently, there are two sectors of the fishery, one that processes the fish onshore and a larger sector using offshore catcher–processor boats (Sylvia and Enriquez 1994). The former fleet is the subject of this study. During this period, fishing effort was restricted by requiring the use of a mid-water trawl, restricting some areas from being fished, and in 1992, fishing was banned between midnight and one-half hour after sunrise local time (B. Wiedoff, Pacific States Marine Fisheries Commission, 2040 SE Marine Science Drive, Newport, OR 97365, U.S.A., personal communication). Restrictions are primarily meant to limit bycatch of salmon and rockfish. Since 1989, stock assessments have not been based on CPUE.

Materials and methods

Information on the 1992–1996 Pacific hake fishery comes from computerized logbook data provided by the Oregon Department of Fisheries and Wildlife. It should be noted that these catches comprise less than half of the total hake landings in Oregon, most of the rest being taken at sea by catcher–processor vessels. Although data from 1990 and 1991 are also available, fleet sizes in those years were too small to be amenable to this analysis (there were five vessels in 1990 and 11 vessels in 1991). The following fields were included in the original data set: a unique vessel identifier; date, time, and port of departure; date, time, and port of return; time, latitude, and longitude of each net set; time that each tow ended and duration of the tow; hailed pounds of hake per tow, and adjusted pounds per tow (total weight of catch, as measured in port, is used to adjust the hailed weights from each tow). Vessel length, tonnage, and horsepower are also known.

Out of a total of 9470 tow records that comprised 5503 trips, 41 trips having tow set locations that were obviously in error are omitted (e.g., ones somewhere in eastern Oregon or in the vicinity of Hawaii), as are 21 other tow records having various types of glaringly incorrect data. The remaining records are used in the calculations of both types of group size (see below). A second data set is constructed by also excluding trips originating from ports other than Astoria and Newport. The excluded trips comprise on average 8.8 trips per year (range 3–20). The resulting second data set is used in statistical analyses of CPUE. A third data set is constructed in which all tows made by infrequent hake fishers are removed. A vessel is considered to be an infrequent hake fisher if the number of tows made by that vessel in a season was more than one standard deviation below the mean number of tows made by all vessels landing hake that year. Finally, a fourth data set is used in statistical analyses in which search time is the dependent variable. Here, tows made by infrequent hake fishers are restored but three other types of tows are removed. These are tows having port departure times of "0000", which represents the default figure for missing data, as well as port departures of midnight. Most of these cases are likely to represent missing data for reasons having to do with the way in which captains fill out the logs. Also excluded were tows with negative search times (largely resulting from data entry errors in which departure times occur after the tow start time). Most importantly, only the first tows of a trip are included in this data set.

Estimation of the variables

Effort is estimated as simply the fishing time, the duration of a tow. Thus CPUE for each tow is calculated as adjusted pounds of hake per tow divided by the duration of the tow. Because records are anonymous, it is necessary to indirectly infer group sizes from the logbook records. Two measures of fishing group, or aggregation, size are estimated in an attempt to distinguish passive, aggregation size from active, information-sharing group size. Aggregation size is here defined as the number of other boats towing in proximity to the focal boat plus one (for the focal vessel). Vessels are considered to be in proximity to each other if the midpoints of their tow times were within 12 h of each other and on the same calendar day and their starting locations were within 5 km. Vessels may actually be towing much closer than 5 km, but because tows themselves may originate fairly far apart (mean duration of tows = 1.8 h), a distance of 5 km between the starting locations is used. Distances of 1 and 15 km (the latter corresponding to mean patch radius according to Dorn (1997)) were also evaluated in preliminary analyses and found to have less predictive power on the whole.

A second measure of group size that is interpreted to reflect the size of a vessel's information-sharing group during any one year is estimated as follows. First, a pair of vessels is considered to have been "near" each other on any given day if they had tow starting locations that were within 5 km of each other and tow starting times within 12 h of each other, otherwise they are counted as having been "far" from each other. For each day (i) of a particular year's fishing season, and where there are V vessels fishing during that season, a $V \times V$ matrix, $\mathbf{M}_i$, was constructed in which each cell contains a one or a zero depending on whether a pair of boats is found to be "near" or "far", respectively. A matrix $\mathbf{M}$ of observed counts of being near is constructed by summing these matrices over all fishing days of the year. Thus, the cell contents of $\mathbf{M}$ are the sum of the corresponding daily matrices $\mathbf{M}_i$. A matrix of the expected number of events of being near is constructed by first taking each daily matrix $\mathbf{M}_i$ and permuting it by randomly reordering the rows and then reordering the columns in the same way as the rows (not randomly). This results in a new matrix $\mathbf{P}_i$. Matrices $\mathbf{P}_i$ are then summed over all fishing days in a year to give a matrix $\mathbf{P}$, the expected frequencies of being near. Next, matrices $\mathbf{M}$ and $\mathbf{P}$ are compared. If the value of a cell in $\mathbf{P}$ is greater than the value of the corresponding cell in $\mathbf{M}$, a value of 1 is assigned and added to the appropriate cell in matrix $\mathbf{C}$. This

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whole process of permuting matrices $\mathbf{P}_i$ and comparing them with $\mathbf{M}_i$ was repeated 100 times, and the result was added to matrix **C** each time. Thus, by the end of the process, if the value of a cell in **P** is always greater than the corresponding cell in **M**, the corresponding cell in **C** will have the maximum value of 100. Finally, cells in matrix **C** are divided by 100 yielding p values indicating whether the null hypothesis can be rejected, the null hypothesis being that the pairs of boats are randomly distributed in space and time. There is an association between that pair of boats when p values are below 0.05. Each vessel's information group size for that year is then the number of statistical associations plus one for itself.

The number of vessels at sea (fishing for hake) on any one day is calculated as the total number of vessels that dropped their nets within 12 h and on the same calendar date as the focal vessel, whether or not they were spatially proximate. Note that this includes only tows and vessels that actually caught hake. Finally, the day of the season for each tow is calculated by counting the number of days from 1 April to the day of the tow.

Regression analyses

Statistical analysis of the relationships between CPUE and each measure of group size is performed separately for each year since a vessel's mean CPUE in one year might be expected to influence their decision to participate in the fishery in subsequent years (Tables 2–3). An initial set of variables are included because they are believed to be relevant and important predictors of CPUE based on prior knowledge and evaluation of pair-wise regressions. Backwards elimination was used to pare down the initial set of variables and arrive at a final set of predictive variables for each year that had significance at $\alpha \leq 0.05$. Independent variables initially included in each regression are port of departure (PD), day of season (SE), day of season squared (SE2), vessel length (VL), vessel tonnage divided by horsepower (THP), and either aggregation size (AG) and aggregation size squared (AG2) or information group size (IG) and information group size squared (IG2). Vessel length and tons·hp^{-1} were both included as vessel length may affect how far from port a vessel travels and tons·hp^{-1} provides a measure of how rapidly the vessel can get there. The quadratic form of day of season is included because hake are migratory, and thus, fish abundance may ebb and flow over the course of the season rather than decline or increase in a strictly linear fashion. Similarly, group size may have a nonlinear relationship with CPUE and hence both group size and group size squared are included in the initial model. To control for nonconstant variance of errors in the preliminary models, the dependent variable CPUE is transformed to $\log_{10}$CPUE. Thus, the initial models are

$$(2)\quad \log_{10}\text{CPUE} = a + b\text{PD} + c\text{SE} + d\text{SE2} + e\text{VL} + f\text{THP} + g\text{AG} + h\text{AG2} + \varepsilon_i$$

$$(3)\quad \log_{10}\text{CPUE} = a + b\text{PD} + c\text{SE} + d\text{SE2} + e\text{VL} + f\text{THP} + g\text{IG} + h\text{IG2} + \varepsilon_i$$

To evaluate the impact of number of vessels at sea on CPUE, similar regression models are constructed replacing the group size variables with number of vessels at sea (VS) and number of vessels at sea squared (VS2). Backward elimination is again used to obtain a final model. The model is tested first with the second data set (which excludes trips that did not originate in Newport or Astoria) and then with the third data set (in which tows made by infrequent hake fishers are removed). The initial model is

$$(4)\quad \log_{10}\text{CPUE} = a + b\text{PD} + c\text{SE} + d\text{SE2} + e\text{VL} + f\text{THP} + g\text{VS} + h\text{VS2} + \varepsilon_i$$

Finally, the relationships between search time and each type of group size are examined using only data from first tows (the fourth data set). Because the Clark and Mangel (1984) model provides an a priori reason to believe that search time should be related to the inverse of group size (AG^{-1} or IG^{-1}), a backward elimination approach is not used and the intercept is suppressed. The regression models are

$$(5)\quad \text{Search time} = a\text{PD} + b\text{SE} + c\text{SE2} + d\text{VL} + e\text{THP} + f\text{AG}^{-1} + \varepsilon_i$$

$$(6)\quad \text{Search time} = a\text{PD} + b\text{SE} + c\text{SE2} + d\text{VL} + e\text{THP} + f\text{IG}^{-1} + \varepsilon_i$$

Results

Mean and range of aggregation size varied only slightly over the years of the study, whereas mean size of information groups increased steadily until 1995, after which it dropped dramatically (Table 1). The year 1993 was somewhat unusual in that the range of group sizes was much narrower than in other years and the modal group size was very low. Vessel length, tonnage, and horsepower increased steadily over the years of the study, reaching a peak in 1995 and dropping somewhat in 1996. CPUE was highest in 1992 with an uneven decline thereafter.

It is found that aggregation size is a significant predictor of CPUE in 1992–1994, but not 1995–1996, whereas the square of aggregation size is significant in 1995 and 1996, but not in 1992–1994 (Table 2). In all years, the coefficient of either aggregation size or its square is positive, indicating that fishers obtain higher CPUE with increasing aggregation size. When information group size is substituted for aggregation size, there is a significant positive relationship between CPUE and group size in years 1992–1995, a significant, positive relationship with the square of information group size in 1996, and a significant, negative relationship with the square of information group size in 1992 and 1995 (Table 3). This suggests that in all years CPUE increases with group size at least initially; however, in 1992 and 1995 CPUE begins to decline with larger group sizes.

In the analysis of the effect of number of vessels at sea on CPUE, when all fishers are included we find no relationship in 1992 and 1996 (Table 4). In 1993, there is a negative, significant effect of vessels at sea on CPUE, whereas in 1995 there is a positive, significant effect. In 1994, the number of vessels at sea has a positive and significant effect on CPUE, whereas the square of vessels at sea has a negative, significant effect. When tows made by infrequent fishers are removed from the analysis, the effect of vessels at sea is negative in 1993, positive in 1995, and of no significance in other years

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Table 1. Fleet and vessel characteristics summarized by year.

	1992	1993	1994	1995	1996
Fleet size	22	17	23	27	28
Length	76.6	77.2	76.2	82.8	79.9
Tonnage	91.7	94.2	97.4	111.8	102.8
Horsepower	574.6	588.6	619.7	734.8	679.4
CPUE	50 429.0	49 790.9	35 106.4	43 960.2	35 460.5
Aggregation size					
Mean	1.1	1.1	1.2	1.1	0.8
Mode	1	1	1	1	1
Range	1–6	1–7	1–7	1–8	1–6
Information group size					
Mean	3.4	3.5	8.5	11.9	2.1
Mode	10	2	10	15	12
Range	1–12	1–8	1–13	1–17	1–17

Note: Fleet size, total numbers of vessels in the fishery; Length, mean vessel length (feet); Tonnage, mean vessel tonnage; Horsepower, mean vessel horsepower (hp); CPUE, catch-per-unit-effort ($lbs \cdot h^{-1}$).

Table 2. Regression of $\log_{10}$CPUE on port of departure, day of season, day of season squared, vessel length, vessel tonnage·hp^{-1}, aggregation size, and aggregation size squared.

		1992	1993	1994	1995	1996
N		1889	1259	1847	1663	1697
Adjusted R^2		0.123	0.088	0.084	0.039	0.136
Port of departure	Coefficient	0.181		–0.177	0.086	0.147
	P	0.0001		<0.0001	<0.0001	<0.0001
Day of season	Coefficient		–0.002	–0.007	–0.001	–0.011
	P		<0.0001	<0.0001	0.0291	<0.0001
(Day of season)^2	Coefficient	<–0.001		<0.001		<0.001
	P	<0.0001		<0.0001		<0.0001
Vessel tonnage·hp^{-1}	Coefficient	–1.034	–0.935	–1.118	–0.655	–1.161
	P	<0.0001	<0.0001	<0.0001	0.0005	0.0001
Vessel length	Coefficient	0.005	0.005		0.004	
	P	0.0025	0.0002		0.0001	
Aggregation size	Coefficient	0.042	0.030	0.039		
	P	<0.0001	<0.0001	<0.0001		
(Aggregation size)^2	Coefficient				0.003	0.004
	P				0.0126	0.0099

Note: Backwards elimination is used and only variables with significance at $\alpha \leq 0.05$ are included.

(Table 5). The square of vessels at sea has no predictive power in any year.

Search time is the dependent variable in the final two analyses reported here. The inverse of aggregation size is found to be significantly, and positively, related to search time in years 1993–1995, indicating that search time does decline with aggregation size in these years (Table 6). The relationship between search time and the inverse of information-sharing group size is significant but negative in 1992, significant and positive in 1993–1995, and insignificant in 1996 (Table 7). It is of interest that from 1993 to 1996 the relationship grows steadily weaker. It should also be noted that although the R^2 values are much higher for these last two analyses than for earlier analyses, the values are not directly comparable because the intercept is suppressed here.

The effects of the other explanatory variables are included in the relevant tables but are not discussed here in keeping with the focus on the relationships between grouping and CPUE, and grouping and search time. Comparisons of the results of primary interest are tabulated in a single table (Table 8).

Discussion

It is found that there are statistically significant, repeated interactions among pairs of vessels. It is possible that these statistical regularities are due solely to the same fishers repeatedly but independently targeting the same favorite fishing spot. Although spatial visualization of the data would add insight into the question, other evidence supports the interpretation of these patterns as being due to information

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Table 3. Regression of $\log_{10}$CPUE on port of departure, day of season, day of season squared, vessel length, vessel tonnage·hp^{-1}, information group size, and information group size squared.

		1992	1993	1994	1995	1996
N		1891	1259	1847	1666	1697
Adjusted R^2		0.120	0.089	0.080	0.062	0.136
Port of departure	Coefficient	0.143		–0.137		0.147
	P	<0.0001		<0.0001		<0.0001
Day of season	Coefficient		–0.001	–0.007		–0.011
	P		<0.0001	<0.0001		<0.0001
(Day of season)^2	Coefficient	<–0.001		<0.001		<0.001
	P	<0.0001		<0.0001		<0.0001
Vessel tonnage·hp^{-1}	Coefficient	–0.962	–0.792	–1.006		–1.161
	P	<0.0001	<0.0001	<0.0001		<0.0001
Vessel length	Coefficient	0.008	0.004		0.002	
	P	<0.0001	0.0047		0.0103	
Information group size	Coefficient	0.065	0.016	0.012	0.059	
	P	<0.0001	<0.0001	<0.0001	<0.0001	
(Information group size)^2	Coefficient	–0.004			–0.003	0.004
	P	0.0005			<0.0001	0.0099

Note: Backwards elimination is used and only variables with significance at $\alpha \leq 0.05$ are included.

Table 4. Regression of $\log_{10}$CPUE on port of departure, day of season, day of season squared, vessel length, vessel tonnage·hp^{-1}, number of vessels fishing for hake at sea, and number of vessels fishing for hake at sea squared, when records from inefficient fishers are included.

		1992	1993	1994	1995	1996
N		1889	1259	1847	1663	1701
Adjusted R^2		0.109	0.079	0.080	0.038	0.133
Port of departure	Coefficient	0.198		–0.145	0.091	0.148
	P	<0.0001		<0.0001	<0.0001	<0.0001
Day of season	Coefficient			–0.006	–0.002	–0.011
	P			<0.0001	0.0063	<0.0001
(Day of season)^2	Coefficient	<–0.001	<–0.001	<0.001		<0.001
	P	<0.0001	<0.0001	<0.0001		<0.0001
Vessel tonnage·hp^{-1}	Coefficient	–1.004	–0.888	–1.099	–0.648	–1.130
	P	<0.0001	<0.0001	<0.0001	0.0006	<0.0001
Vessel length	Coefficient	0.004	0.004		0.004	
	P	0.0052	0.0046		<0.0001	
Vessels at sea	Coefficient		–0.010	0.057	0.006	
	P		0.0148	<0.0001	0.0394	
(Vessels at sea)^2	Coefficient			–0.005		
	P			<0.0001		

Note: Backwards elimination is used and only variables with significance at $\alpha \leq 0.05$ are included.

sharing. At the very least, groups are composed of fishers from more than one port, suggesting that fishers do not simply visit the nearest fishing grounds. Furthermore, some Newport fishermen indicated that they do share information, as is the case in many other fisheries in which the fish are patchily distributed (Ruttan 1999). In addition, some of these fishers claim to share information principally with other vessels delivering to the same processor. In this light, Cove's (1973) description of competitive strategies among non-owner operators working for the same processor is interesting. In his description of Newfoundland offshore fisheries in the 1960s, the only instance of information sharing occurred between captains who did not work for the same processor; he argued that this occurred because they were not competing for the

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Table 5. Regression of $\log_{10}$CPUE on port of departure, day of season, day of season squared, vessel length, vessel tonnage·hp^{-1}, number of vessels fishing for hake at sea, and number of vessels fishing for hake at sea squared, when records from inefficient fishers are excluded.

		1992	1993	1994	1995	1996
N		1783	1126	1528	1443	1451
Adjusted R^2		0.120	0.081	0.073	0.036	0.128
Port of departure	Coefficient	0.172		–0.134	0.075	0.148
	P	<0.0001		<0.0001	0.0006	<0.0001
Day of season	Coefficient	–0.002		–0.009	–0.002	–0.010
	P	<0.0001		<0.0001	0.0070	<0.0001
(Day of season)^2	Coefficient		<–0.001	<0.001		<0.001
	P		<0.0001	<0.0001		<0.0001
Vessel tonnage·hp^{-1}	Coefficient	–1.024	–0.989	–0.909	–0.776	–1.245
	P	<0.0001	<0.0001	<0.0001	0.0011	<0.0001
Vessel length	Coefficient		0.004		0.003	
	P		0.0295		0.0010	
Vessels at sea	Coefficient		–0.009		0.007	
	P		0.0354		0.0375	
(Vessels at sea)^2	Coefficient					
	P					

Note: Backwards elimination is used and only variables with significance at $\alpha \leq 0.05$ are included.

Table 6. Regression of search time on port of departure, day of season, day of season squared, vessel length, vessel tonnage·hp^{-1}, and the inverse of aggregation size.

		1992	1993	1994	1995	1996
N		459	258	468	409	536
Adjusted R^2		0.939	0.898	0.937	0.890	0.824
Port of departure	Coefficient	–1.927	115.466	97.106	46.780	12.278
	P	0.9256	<0.0001	<0.0001	0.0018	0.7006
Day of season	Coefficient	5.919	–0.874	0.366	3.710	6.401
	P	<0.0001	0.2715	0.3329	0.0002	<0.0001
(Day of season)^2	Coefficient	–0.021	0.005	0.001	–0.022	–0.028
	P	<0.0001	0.2043	0.6591	0.0020	0.0001
Vessel tonnage·hp^{-1}	Coefficient	–360.850	–972.550	100.493	2.470	–508.251
	P	0.2628	<0.0001	0.1611	0.9842	0.0840
Vessel length	Coefficient	4.805	4.765	2.224	1.606	3.127
	P	<0.0001	<0.0001	<0.0001	0.0025	0.0108
(Aggregation size)$^{-1}$	Coefficient	27.616	93.800	24.898	50.599	21.677
	P	0.3127	<0.0001	0.0357	0.0039	0.5157

Note: Only first tows of each trip are included. Backwards elimination is not used and the intercept is suppressed.

best vessels and crew. The difference in strategy on the part of Newport fishers may be due to the fact that many are owner operators, and they claim to have an interest in ensuring that the capital-intensive, surimi processing facilities stay afloat, so to speak. Because hake degrades quickly, processors prefer to avoid gluts of fishing arriving at the docks, and in turn, fishers avoid keeping fish in the hold for long periods even if it means returning to port without a full load. A finer-grained analysis of the actual dynamics of interaction between fishers in the hake fishery would shed much light on these issues.

In the years 1993 to 1995, fishers also appear to have benefitted from grouping by reducing their time spent searching. There was a positive association between search time and the inverse of both aggregation size and information-sharing group size in each of these years. In 1992, there was, however, a negative effect of group size on search time, and in 1996, there was no effect whatsoever. Several explanations can be offered. First, on the one hand, the smaller sample sizes used in the analysis of search time may have lowered the statistical power enough to dilute the effect, particularly in 1996. On the other hand, the results from 1996 appear to fit

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Table 7. Regression of search time on port of departure, day of season, day of season squared, vessel length, vessel tonnage·hp^{-1}, and the inverse of information group size.

		1992	1993	1994	1995	1996
N		460	258	468	410	539
Adjusted R^2		0.940	0.899	0.937	0.889	0.825
Port of departure	Coefficient	–44.714	115.668	85.101	48.089	9.736
	P	0.0512	<0.0001	<0.0001	0.0017	0.7599
Day of season	Coefficient	4.768	–1.043	0.401	3.652	6.788
	P	<0.0001	0.1884	0.2842	0.0003	<0.0001
(Day of season)^2	Coefficient	–0.017	0.005	0.001	–0.023	–0.030
	P	<0.0001	0.2550	0.6889	0.0016	<0.0001
Vessel tonnage·hp^{-1}	Coefficient	134.631	–2836.592	104.942	–139.706	–420.371
	P	0.6923	<0.0001	0.1418	0.3207	0.1621
Vessel length	Coefficient	5.706	8.548	2.328	2.268	2.779
	P	<0.0001	<0.0001	<0.0001	<0.0001	0.0253
(Information group size)$^{-1}$	Coefficient	–148.768	338.567	40.111	36.138	65.701
	P	0.0001	<0.0001	0.0051	0.0508	0.1181

Note: Only first tows of each trip are included. Backwards elimination is not used and the intercept is suppressed.

Table 8. Comparison of effects of aggregation size and information group size on (*a*) $\log_{10}$CPUE and (*b*) search time. Note that the effects of vessels at sea and vessels at sea squared are reported from analyses including (1) all fishers and (2) only efficient fishers.

	1992	1993	1994	1995	1996
(*a*) $\log_{10}$CPUE					
Aggregation size	(+) ***	(+) ***	(+) ***		
(Aggregation size)^2				(+) *	(+) **
Information group size	(+) ***	(+) ***	(+) ***	(+) ***	
(Information group size)^2	(–) ***			(–) ***	(+) **
(1) Vessels at sea		(–) *	(+) ***	(+) *	
(1) (Vessels at sea)^2			(–) ***		
(2) Vessels at sea		(–) *		(+) *	
(2) (Vessels at sea)^2					
(*b*) Search time					
(Aggregation size)$^{-1}$		(+) ***	(+) *	(+) **	
(Information group size)$^{-1}$	(–) ***	(+) ***	(+) **	(+) *	

Note: Asterisks denote levels of significance: *, $\alpha \leq 0.05$; **, $\alpha \leq 0.01$; ***, $\alpha \leq 0.001$. The sign of each variable's coefficient is in parentheses.

a trend of declining importance of information sharing. Perhaps as fishers acquired experience and skill in the fishery and with technological improvements in fish-finding gear, they began to rely less and less on information-sharing networks. Notably, this would improve the fit of CPUE-based stock assessments if it means that captains are searching out a larger number of patches rather than congregating at a few. Second, one may question the applicability of the Clark and Mangel (1984) model to this fishery. In retrospect, there are reasons to believe that reductions in search time may not be the primary motivation for forming information-sharing groups, and though the Clark and Mangel model of information sharing provided a useful starting point, it may not be the most appropriate framework for analyzing this particular fishery. Firstly, their model includes an implicit assumption that foragers search simultaneously until one finds a patch, after which they all converge. Here, fishermen report that vessels that are about to return to port share information with those just heading to sea. This permits the group to maintain contact with a moving patch and allows vessels to provide the processor with a continuous stream of fresh fish. The fact that fishers do not necessarily stay on the patch until their hold is full is yet another violation of the assumptions underlying the model. In addition, hake fishers may not be strict CPUE maximizers. As has been mentioned repeatedly, they may be attending to numerous other features of the catch such as the mean and variance of fish size. Hence, it is problematic that patch quality is not included in the Clark and Mangel model. Furthermore, although it has been the implicit assumption in this paper that fishers who minimize search time and maximize CPUE incur the least costs and thus obtain the greatest net profits, we do not have any evidence for this. This lack of attention to actual costs has also been criticized in studies of nonhuman foraging (Creel and Creel 1995; Packer and Caro 1997). Finally, modern technology available to human foragers makes it easier

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to predict the location of fish schools without sharing information, particularly because hake migrate along fairly well-defined thermoclines. This may explain the declining importance of information-sharing groups even as those groups still obtained high CPUE.

Results provide clearer support for the hypothesis that vessels in groups, or aggregations, catch more per unit of effort. In all years, CPUE increases with aggregation size or its square or with group size or its square. There is some suggestion that information-sharing groups can grow too large, as evidenced by patterns in 1992 and 1995. In these years, CPUE has a positive relationship with information-sharing group size but a negative relationship with its square. There are two alternative explanations for this pattern of results. First, fishers benefit from sharing or gleaning information from others. By doing so, they are able to target high-quality patches of fish. Alternatively, the result may be a simple artifact of more vessels joining the fishery when the fishing is good. If that is true, then one could expect to find a positive correlation between CPUE and the number of other vessels at sea. Such a positive relationship is in fact observed in 1994 and 1995; in 1994, however, the quadratic factor is negative. In 1993, the relationship between CPUE and number of vessels at sea is actually negative.

Good fishing conditions may not be the only reason that more vessels put to sea and fish for hake on a given day. More fishers may target hake when other fisheries are closed. Presumably these infrequent hake fishers are also less efficient. Thus, the negative relationship between CPUE and number of vessels in 1993 and between CPUE and the square of number of vessels in 1994 leads one to wonder whether this provides evidence of competitive effects in the fishery or simply of inefficient fishers entering the fishery. In the former case, we would expect the CPUE of all fishers to decline with increasing numbers of vessels at sea fishing for hake, whereas in the latter case, the CPUE of frequent fishers would be expected to remain relatively high. When tows made by infrequent fishers are removed from analysis, relationships between CPUE and both vessels at sea and its square are removed for the year 1994. The patterns for 1993 and 1995 are unaffected. This suggests that in 1993, there was a genuine effect of competition on all vessels that occurred as more vessels entered the fishery. In contrast, in 1994, the effects of both vessels at sea and vessels at sea squared on CPUE appear to have been due to inefficient fishers entering the fishery. The year 1995 appears to have been the only year in which the high CPUE associated with larger groups may have been an artifact of more vessels drawn to bountiful conditions in the fishery. It is notable that in 1995, total allowable catch was attained unusually early in the season; the last departure date was in late July, whereas in other years, the season ended sometime between early September and mid-November. These results lead to the conclusion that in all years, with the possible exception of 1995, fishers actually benefit from fishing in aggregations or sharing information with others, presumably because they are able to find higher-quality patches. It also suggests that an ideal free distribution of fishing group sizes has not yet formed in this relatively new fishery.

In conclusion, there is support for the hypothesis that information sharing, or even passive aggregation, on the part of fishermen influences CPUE. This suggests that some caution should be exercised when using CPUE-based stock assessment. Although it is possible that this relationship would have a minimal effect in an established fishery, more pronounced distortions may be found in newly established fisheries, exactly those in which we have the fewest independent estimates of stock size. In these fisheries, fishers may still be learning how to fish (and thus maintaining or even raising CPUE independent of stock size) and they are also in the process of establishing information networks. The purpose of these networks is specifically to help fishermen avoid randomly sampling the environment. It should be noted that this paper is not meant to specifically critique the management of hake in Oregon (especially as it is no longer CPUE based), but rather to draw attention to the problems that this method poses.

A second point worth emphasizing is that fishers may be benefitting from sharing information, or gleaning information by observation, through reductions in search time and (or) an increased ability to find high-quality patches. Foraging theory has focused principally on the former, doubtless because it is harder to guess what constitutes quality for non-human foragers. Detailed ethnographic studies on searching strategies would provide a better understanding of the precise economic benefits to be gained from pursuing these strategies.

Finally, there may be considerable variation in behavioral strategies that corresponds with yearly environmental variability. We should expect this particularly for species in which recruitment is believed to be more strongly correlated with environmental conditions than with spawning stock size, as is the case for Pacific hake (Francis et al. 1989). Additional work relating behavioral strategies to environmental variability would be valuable.

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List of symbols

$f(n)$	gross rate of return (weight per unit time)
C	forager's gut capacity
n	forager group size
m	number of "meals" in a patch
B	patch size (weight)
θ	minimum of 1 or $m \cdot n^{-1}$
τ	the time spent harvesting a patch of given size
λ	patches found per unit time
PD	port of departure
SE	days elapsed since 1 April
SE2	days elapsed since 1 April squared
VL	vessel length
THP	vessel tonnage divided by horsepower
AG	aggregation size
AG2	aggregation size squared
IG	information group size
IG2	information group size squared
VS	total number of vessels catching hake on a given day
VS2	total number of vessels catching hake on a given day squared

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The effects of adjacent land use on wetland amphibian species richness and community composition

Jeff E. Houlahan and C. Scott Findlay

Abstract: Habitat destruction and fragmentation have been identified as possible causes of large-scale amphibian declines. Here, we examine the effects of adjacent land use and water quality on wetland amphibian species richness, abundance, and community composition in 74 Ontario wetlands. Species richness was positively correlated with wetland area, forest cover, and the amount of wetlands on adjacent lands and negatively correlated with road density and nitrogen levels. The land-use effects peak at 2000–3000 m. Amphibian abundance was positively correlated with forest cover, distance to wetlands >20 ha, and amount of marsh habitat and negatively correlated with road density. The effects of adjacent land use were strongest at around 200 m. Land-use and water quality effects varied widely across species, although most species are positively correlated with forest cover and amount of wetlands on adjacent lands and negatively correlated with road density and water quality. These results suggest that the effects of adjacent land use on amphibian communities can extend over comparatively large distances. As such, effective wetland conservation will not be achieved merely through the creation of narrow buffer zones between wetlands and intensive land uses, but rather will require maintaining a heterogeneous regional landscape containing relatively large areas of natural forest and wetlands.

Résumé : La destruction et la fragmentation des habitats sont considérés comme des causes possibles du déclin à grande échelle des amphibiens. Nous avons étudié les effets de la qualité de l'eau et de l'utilisation des territoires adjacents sur la richesse en espèces, l'abondance et la composition des communautés d'amphibiens de 74 terres humides de l'Ontario. La richesse en espèces est en corrélation positive avec la surface de la terre humide, le couvert forestier et l'importance des terres humides dans les territoires adjacents et en corrélation négative avec la densité des routes et les concentrations d'azote. Les effets de l'utilisation des terres atteignent un maximum à 2000–3000 m. L'abondance des amphibiens est en relation positive avec le couvert forestier, la distance des terres humides >20 ha et l'importance des habitats marécageux et en relation négative avec la densité des routes. Les effets de l'utilisation des territoires adjacents sont maximaux à environ 200 m. Les effets de l'utilisation des terres et de la qualité de l'eau varient considérablement d'une espèce à l'autre, bien que la plupart des espèces montrent une corrélation positive avec le couvert forestier et l'importance des terres humides dans les territoires adjacents et une corrélation négative avec la densité des routes et la qualité de l'eau. Ces résultats indiquent que les effets de l'utilisation des territoires adjacents sur la communauté d'amphibiens peuvent se faire sentir sur des distances relativement grandes. La conservation efficace des terres humides ne pourra donc pas s'effectuer seulement par l'établissement d'étroites bandes tampons entre les terres humides et les territoires à utilisation intensive; il faudra maintenir un paysage régional hétérogène contenant des surfaces relativement importantes de forêts naturelles et de terres humides.

[Traduit par la Rédaction]

Introduction

Global amphibian declines have received considerable attention in the last decade (Pechmann et al. 1991; Houlahan et al. 2000; Kiesecker et al. 2001). The list of potential causes include larger-scale stressors such as climate change (Pounds et al. 1999; Kiesecker et al. 2001), increased ultraviolet-B (UV-B) exposure (Blaustein et al. 1998; Broomhall et al. 2000), acid rain (Long et al. 1995; Watkins-Colwell and Watkins-Colwell 1998), ubiquitous pathogens (Lips 1998; Carey 2000), and their interaction (Kiesecker et al. 2001), as well as smaller-scale (local) stressors such as habitat destruction (Findlay and Houlahan 1997; Semlitsch 2000), habitat degradation and (or) fragmentation (Findlay and Houlahan

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1997; Semlitsch 2000), pesticide and fertilizer application (Hecnar 1995; Bridges and Semlitsch 2000; Davidson et al. 2001), introduced species (Adams 1999; Lawler et al. 1999), and road mortality (Fahrig et al. 1995; Hels and Buchwald 2001). Reversing or stabilizing declines requires that we identify the relative importance of larger-scale versus smaller-scale stressors and, as a result, the extent to which the problem can be mitigated by local conservation management.

Most smaller-scale stressors associated with amphibian decline are related to changes in land use. Their local nature notwithstanding, these stressors have the potential to be key factors in larger-scale amphibian declines because deforestation, desertification, wetland destruction, increased road density, and urbanisation are ubiquitous and global in nature. Globally, about 25% of the land historically covered by forest has been deforested, and of the remaining 75%, less than half represents intact forest ecosystems (Nebel and Wright 2000). As many as 50% of the world's wetlands have been destroyed in the last century (Organisation for Economic Cooperation and Development / The World Conservation Union (OECD/IUCN) 1996) with declines of ~50% in the United States (Frayer et al. 1983; Patrick 1994) and southern Canada (Lynch-Stewart 1983) and ~75% in southern Ontario (Ontario Ministry of Natural Resources (OMNR) 1992).

For many amphibian species, loss and degradation of wetlands is a major threat. In eastern Ontario, 14 of the 15 relatively common amphibians are aquatic breeders, with wetlands constituting the majority of breeding habitat (Hecnar and M'Closkey 1998). Destruction of wetland habitat will directly affect amphibian populations, but more subtle effects associated with incompatible adjacent land uses may also degrade wetlands making them unsuitable as breeding environments for some amphibian species. In southeastern Ontario, the major anthropogenic modifications to both wetlands themselves and adjacent lands include deforestation and (or) conversion to agricultural use, road construction, wetland drainage and in-filling, and urbanization. These changes in land use are often associated with fertilizer and herbicide application, wastewater runoff, and livestock waste. Such changes may result in reduction or degradation of critical terrestrial habitat (Hecnar and M'Closkey 1998; Ross et al. 2000), impede migration among local populations (Gibbs 1998*b*; deMaynadier and Hunter 2000), increase mortality through road kill (Fahrig et al. 1995; Hels and Buchwald 2001), and destroy or degrade breeding habitat by modifying wetland hydrology (Wilbur et al. 1996; Euliss and Mushet 1996) or increasing eutrophication (Detenbeck et al. 1996; Crosbie and Chow-Fraser 1999).

Here we present the results of extensive amphibian surveys carried out in 75 wetlands in southeastern Ontario. The study had two objectives: (*i*) to identify the strength and nature of associations between wetland amphibian community structure, composition, and adjacent land-use elements and (*ii*) to identify the spatial scale at which adjacent land-use impacts operate. The importance of the latter cannot be underestimated: effective wetland conservation, indeed biodiversity conservation in general, requires an understanding of what the key anthropogenic stressors are, their relative importance, and the scales at which they operate. If wetland amphibian communities are affected by adjacent land use, then practical conservation management will require changes in how adjacent lands are managed. Land-use planners and regulators will then need to know on which lands such changes must be effected. By explicitly considering the question of characteristic spatial scales, our results will (*i*) inform the development of scientifically based land-use policy and regulations at regional and provincial levels and (*ii*) provide a useful resource for assisting land-use planners and resource managers in estimating the effects of proposed changes in adjacent land use on amphibian species richness and community composition at specific sites.

Methods

General description of wetland sites

We sampled 75 wetlands from southeastern Ontario between 44′12″ and 45′51″ latitude and 74′34″ and 76′30″ longitude (Fig. 1). This area is in the humid high cool temperate climatic region of Canada with a mean annual temperature of 4.2 °C, mean annual precipitation of ~800 mm, and an average of 117 frost-free days annually (Ecoregions Working Group 1989). About 60–70% of southeastern Ontario land area is forest-covered, and these forests are dominated by sugar maple (*Acer saccharum*), yellow birch (*Betula lutea*), hemlock (*Tsuga canadensis*), and white pine (*Pinus strobus*). Almost all wetlands contained swamp and marsh habitat and nine contained some fen and (or) bog habitat. The dominant swamp plants were silver maple (*Acer saccharinum*), cedar (*Thuja occidentalis*), dogwood (*Cornus* spp.), willows (*Salix* spp.), alder (*Alnus rugosa*), and ash (*Fraxinus* spp.). Dominant marsh plants included cattails (*Typha* spp.), purple loosestrife (*Lythrum salicaria*), aquatic macrophytes (*Hydrocharis morsus-ranae*, *Nuphar*, *Nympheae*, *Potamogeton* spp.), and grasses and sedges (*Calamagrostis canadensis*, *Leersia oryzoides*, *Phalaris arundinacea*, *Carex* spp., *Scirpus* spp.). The bogs and fens were dominated by leatherleaf (*Chamaedaphneae calyculata*), blueberries and cranberries (*Vaccineum* spp.), sedges (*Carex* spp.), and cottongrass (*Eriophorum* spp.). Most of the sampled wetlands were in the St. Lawrence lowlands and are underlain by Paleozoic rock, but several in the northwestern corner of the study area are at the edge of the highlands and have Precambrian metamorphic bedrock (Fulton et al. 1987). Mean wetland size was 66.7 ha: 56 wetlands were palustrine, 10 were lacustrine, and nine were riverine. The wetlands occurred along a wide gradient of land-use intensity from urban wetlands (located near the heart of Ottawa, Ont.) to relatively remote wetlands in the Pakenham Hills, (~80 km west of Ottawa).

Species descriptions

Seventeen amphibian species are found in eastern Ontario, including 10 anurans (*Rana sylvatica*, *Pseudacris crucifer*, *Pseudacris triseriata*, *Rana pipiens*, *Bufo americanus*, *Hyla versicolor*, *Rana palustris*, *Rana clamitans*, *Rana septentrionalis*, and *Rana catesbeiana*) and seven urodeles (*Ambystoma maculatum*, *Ambystoma laterale*, *Ambystoma jeffersonianum*, *Notophthalmus. viridescens*, *Plethodon cinereus*, *Eurycea bislineata*, and *Hemidactylum scutatum*). All except *P. cinereus* and *E. bislineata* are aquatic breeders (Conant and Collins 1991). The larval forms of all aquatic breeders except *N. viridescens* are aquatic, and several species (e.g., *R. sep-*

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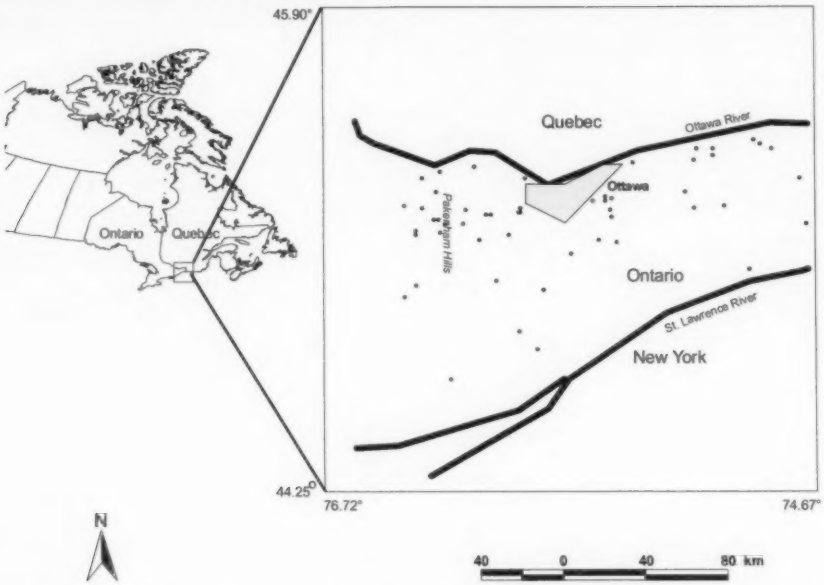
Fig. 1. Map of the study area in southeastern Ontario, Canada.



tentrionalis, *R. catesbeiana*, and *R. clamitans*) spend virtually their entire life cycle in and around open water. Other species (*A. maculatum*, *A. laterale*, *R. sylvatica*, *H. versicolor*, and *B. americanus*) spend a relatively short time during their breeding period in water and are predominately terrestrial (Conant and Collins 1991).

Species richness and abundance

We accumulated species lists during four field seasons (1997–2000) using call surveys, sight surveys, and larval dip-netting. Seventeen wetlands were call and sight surveyed in the first season (1997), and 29 were surveyed in each of years 2 (1998) and 3 (1999). Most dip-netting surveys were completed in the spring of the fourth year (2000), as were some additional call surveys. Call surveys involved at least three visits to each wetland after sunset in early to mid-April, early to mid-May, and June–July to assess early- (e.g., *Hyla crucifer* and *P. triseriata*), mid- (e.g., *R. pipiens* and *B. americanus*), and late-season (e.g., *R. clamitans* and *R. septentrionalis*) breeders, respectively. Several species (notably *P. triseriata* and *R. sylvatica*) call for very short periods in the early spring and are easily missed in time-constrained sight surveys; therefore surveys were repeated in the spring of 2000 in wetlands for which these species had not been previously recorded to ensure that we had not simply missed their breeding season.

Between 1.5 and 40 person-hours were spent in each wetland conducting daytime sight surveys, with search time increasing with the size of the wetland ($\log_{10}$effort = 0.39 + 0.52($\log_{10}$area)). For sight surveys, each wetland was visited three times, once in May to early June, once in mid-June to July, and once in August to early September. During the sight surveys, we turned over rocks and logs searching for urodeles that would not be identified using call surveys, as well as noting any anurans disturbed during search periods.

Although some larval dip-netting was done in the first three years, most of the intensive work was done in June 2000, after the eggs of most species had hatched but before metamorphosis and movement out of breeding habitats. Because of the timing of dip-netting, some late breeders (*R. clamitans*, *R. septentrionalis*, and *R. catesbeiana*) may have been missed. However, these species have extended calling periods and are not cryptic and hence were almost certainly found using call and sight surveys. We spent about 30–60 min dip-netting at each wetland, depending on the number and size of ponds. All larvae were identified using Watermolen and Gilbertson's (1996) key for Wisconsin's larval amphibians.

In addition to presence/absence data, beginning in 1998, we also collected abundance data by counting all amphibians observed during all wetland censuses and dividing by search effort (in hours), yielding an estimate of amphibians seen per hour for each of three visits to all 58 wetlands censused in the second and third years of the study. We then calculated the mean number of amphibians seen per hour across all three visits. Because many adult amphibians are small and cryptic (e.g., *P. crucifer* and *P. triseriata*), subterranean (e.g., *A. maculatum* and *A. laterale*), or present at a relatively small number of wetlands (e.g., *R. septentrionalis* and *R. catesbeiana*), abundance values reflect primarily the abundance of the most common and visible species, *R. pipiens* and *R. clamitans*.

Wetland soil and water nutrients

Sediment and water samples were collected at 72 and 73 wetlands, respectively, during the period from 1997 to 1999. Each wetland was visited three times in 1997, 1998, or 1999 between the beginning of May and the end of August. One water sample was collected during each visit, yielding three water samples per wetland. For 14 wetlands, there was no standing water on the last visit, and for those wetlands, we have only two water samples. Each water sample was a com-

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posite sample taken from four or five different points throughout the wetland. Although composite sampling methods do not provide detailed information about spatial and temporal variability of water quality, they have been identified as a cost- and labor-efficient method of accurately estimating population means (Brown and Fisher 1972; Edland and van Belle 1994). Where possible, we took samples for each visit from about the same locations; this was not always possible because areas with standing water changed from visit to visit. Water was sampled by holding the water bottle vertically 10–40 cm below the surface of the water column. All water samples were immediately acidified with sulfuric acid in the field to a pH < 2.0 (1 mL H_2SO_4 : 50 mL water) and then refrigerated. All samples were analysed within 3–6 months for total phosphorus (TP) and total Kjeldahl nitrogen (TKN) using standard colorimetric methods (American Public Health Association (APHA) 1995). We then calculated mean TP and TKN values in $mg \cdot L^{-1}$ for each wetland.

Four sediment samples were collected in each wetland on the second visit to the wetland, usually in late June or July. We attempted to sample from a wide range of vegetation communities so as to span the full range of sediment nutrient values found in each wetland. The top ~10 cm of sediment was scooped into a small plastic bag, and all sediment samples were immediately frozen upon returning to the lab. All sediment samples were analysed within 3–18 months of the sampling period. Seven samples were lost in transit between the freezer and the sediment analysis laboratory, so seven of the wetlands have only three samples. Soils were dried at 35 °C for 24 h in a forced-air oven. Extremely wet samples were dried for an additional 24 h until completely dry. Samples were then crushed with a wooden rolling pin and sieved through a 2-mm stainless steel sieve. All sediment samples were analysed for total extractable phosphorus (TEP; sodium bicarbonate extraction), ammonium (NH_4; KCl extraction), nitrate (NO_2; KCl extraction), potassium (K; ammonium acetate extraction), and magnesium (Mg; ammonium acetate extraction) (see Appendix A for a detailed description of sediment analyses). We then estimated mean TEP, K, and Mg in $mg \cdot L^{-1}$ and $mg \cdot kg^{-1}$ and mean NH_4 and NO_3 in $mg \cdot kg^{-1}$ for all wetlands.

Land use

For all 75 wetlands, wetland characteristics (area, latitude, longitude, streams, presence of permanent ponds, and percentage of wetland that was marsh, swamp, bog, or fen) and adjacent land use (i.e., road density, forest cover, building density, proportion of lakes or rivers, proportion of wetlands, and distance to nearest wetland) were extracted using Arcview 3.2 (ESRI, 380 New York St., Redlands, CA 92373-8100) and digital 1:10 000 Ontario base maps from the Ontario Ministry of Natural Resources that were created from 1991 aerial photos. Because one of our goals was to estimate the distance at which adjacent land uses affect wetland amphibian communities, we needed to sample at multiple scales. To obtain fine-scale estimates of land-use effects and be reasonably certain that we had land-use data out beyond which land use has little effect, we needed to sample at small to large scales. The largest scale (i.e., 4000 m) was chosen because recent work suggests that land use to 2000 m and beyond can affect amphibian species richness (Findlay and Houlahan 1997; Hecnar and M'Closkey 1998). Thus, values for each variable were estimated for a series of overlapping contours spanning distances of 0–100, 0–200, 0–250, 0–300, 0–400, 0–500, 0–750, 0–1000, 0–1250, 0–1500, 0 –1750, 0–2000, 0–2250, 0–2500, 0–3000, and 0–4000 m from the wetland edge.

Measures related to agricultural practices (e.g., fertilizer and chemical application) were obtained from the 1996 Statistics Canada Census of Agriculture database. These data are provided only at the level of enumeration areas (EA), that is, geographic areas canvassed by one census representative and the smallest geographic area for which census data are reported. EAs are delineated by number of dwellings rather than physical size, and where there were fewer than 15 farms in a single EA, Statistics Canada combined adjacent EAs (for reasons of data confidentiality) so that information is not available for blocks of fewer than 15 farms. The average size of the EAs used in this study was 6406 ha (1388 – 46 592 ha). To estimate the amount of cropped land, chemical application, etc., we calculated the proportion of the EA that fell within the distance contour of interest (i.e., 2000, 3000, or 4000 m) and multiplied that proportion by the total amount of cropped land, chemicals applied, etc., in the entire EA. Clearly, this will introduce some (exactly how much is unknown) measurement error in these variables, as the calculation assumes that chemicals and fertilizers are applied uniformly across the EA.

Statistical analysis

Simple linear regressions were used to examine the bivariate relationships between water and sediment nutrients and each of the independent variables. Multiple regression models were developed by including all independent variables that had bivariate relationships with $p < 0.2$ and removing variables that were not statistically significant at the $\alpha = 0.05$ level. Variable preselection on the basis of bivariate correlation strength is problematic because (*i*) marginal correlations between an independent and dependent variable may be low even though the independent variable has a significant effect when other important correlates are controlled and (*ii*) some independent variables will be correlated with the dependent variable by chance alone. To mitigate the effects of using marginal relationships as a selection criterion, independent variables for which there were theoretical and (or) empirical reasons to expect an effect on water quality (but which were not correlated with the dependent variables at $p < 0.2$) were included in the regression models

Because stepwise regression may be unreliable for detecting the most appropriate models (Miller 1984), for a subset of the regressions, we deleted nonsignificant variables using several different sequences for variable deletion including backwards, forwards, and unordered deletion. In no case did the sequence of variable removal affect the final model.

We used model 1 regression (i.e., ordinary least squares (OLS)), because in most cases, it was a reasonable assumption that error on the dependent variable was at least three times as large as the error on the independent variables (Legendre and Legendre 1998). Moreover, many alternatives to model 1 regression (e.g., standard major axis regression) rely on assumptions about independent variable error that are

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equally difficult to test, thus leaving few objective grounds for choosing the effect estimates of one model over another (Prairie et al. 1995). For consistency, we used model 1 regression even for the few independent variables that we suspect may have relatively large error. We also used Poisson regression for a subset of the analyses, but because the Poisson and model 1 OLS regression results were qualitatively the same and because the data violated a key assumption of Poisson regression (i.e., $\mu = \sigma^2$), we only present the model 1 results.

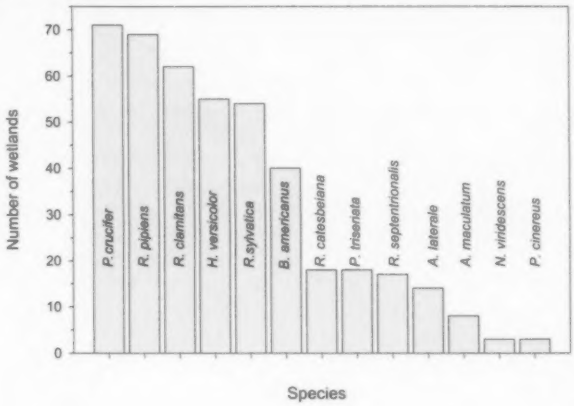
The effects of forest cover, road density, building density, and agricultural intensity on water and sediment nutrient levels were tested using one-tailed hypothesis tests because we expected the relationship to be in a specific direction. Tests of all other independent variables were two-tailed.

For spatially delimited ecosystems (e.g., surface water courses, forest patches, wetlands), an important issue in conservation land-use planning is the distance beyond which putative land-use stressors have no significant effect on the ecosystem attribute in question. This can be determined by assessing changes in model fit with distance from the defined boundary of the ecosystem (Hunsaker and Levine 1995; Findlay and Houlahan 1997). For example, to identify the critical distance for forest cover, we would construct multiple regression models that are identical except for the scale of the forest cover variable. If forest cover on lands beyond a certain critical distance from a wetland has no significant impact on amphibian species richness, then inclusion of information about forest cover beyond that critical distance in the regression model should not improve the fit of a model that predicts amphibian species richness. In fact, when using spatially cumulative measures of land use, including land-use information beyond the critical distance would be expected to reduce model fit, as the additional information contributes only statistical noise. On the other hand, for distances smaller than the critical distance, including information about land use at greater distances should increase model fit.

The type I error rate for individual hypotheses was set at 0.05 despite the comparatively large number of comparisons. The intent of multiple comparison corrections is to reduce the experimentwise probability of making a type I error. But by reducing the type I error rate, the type II error rate is increased. It is not clear, in this context at least, that the negative consequences of committing a type II error are less dramatic than those of committing a type I error. In fact, one might argue that a type I error (finding a significant effect where none exists) implies the short-term financial cost of taking conservation action when none is necessary, whereas a type II error (missing a significant effect when one exists) implies the potential long-term and irreversible impacts of not taking action when it is required.

Spatial autocorrelation is often encountered in ecological data (Lichstein et al. 2002), and so controlling for spatial autocorrelation is often recommended. Visual examinations of correlograms show no evidence that amphibian species richness values are spatially autocorrelated at the landscape scales that we are examining. For spatial autocorrelation to affect the significance of regression coefficients, both dependent and independent variables must be spatially autocorrelated (Legendre et al. 2002). Because there is no evidence that these data are spatially autocorrelated and because spatial autocorrelation does not necessarily bias statistical analyses (Diniz et al. 2003), we have chosen not to control for spatial autocorrelation.

Fig. 2. Occurrence of amphibian species in 75 southeastern Ontario wetlands.



Redundancy analysis (RDA) was used to ordinate amphibian species occurrence along environmental and land-use gradients. RDA is analogous to multiple regression with several dependent variables: the dependent variables (e.g., species presence/absence) are ordinated such that the resulting vectors are linear combinations of the explanatory (e.g., land-use and nutrient variables) and response variables (Legendre and Legendre 1998). RDA provides a visual representation of the propensities of individual species for specific environmental conditions. *Notophthalmus viridescens* and *P. cinereus* were excluded from these analyses because they were only found in 3 of 75 wetlands. As well, we used chi-square and logistic regression to develop species-specific models for predicting species presence based on the environmental and land-use variables.

Amphibian species richness, road density and distance from the wetland variables, and all soil and water nutrient variables were $\log_{10}$ transformed to reduce heteroscedasticity, whereas proportion wetland and buildings were square root transformed.

Results

Species richness

All aquatic breeding species known from southeastern Ontario (Conant and Collins 1991), except *Ambystoma jeffersonianum* and *Rana palustris*, were found in at least one wetland, with richness ranging from 3 to 10 (average 5.8 ± 1.6). The most common species, *P. crucifer*, was found in 71 of 75 (95%) wetlands, and the least common species, *N. viridescens* and *P. cinereus*, were found in 3 of 75 (4%) wetlands (Fig. 2).

Land use

Amphibian species richness showed statistically significant bivariate relationships with a number of land-use vari-

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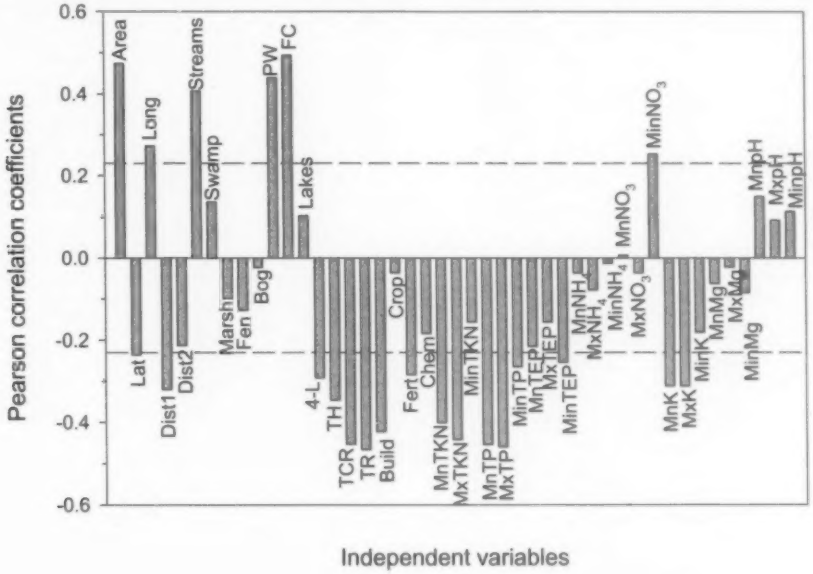
Fig. 3. Correlation coefficients for all independent variables used in amphibian species richness regression analyses. The upper and lower broken lines indicate statistical significance at $\alpha = 0.05$. Area, wetland area; Lat, latitude; Long, longitude; Dist1, distance to nearest wetland; Dist2, distance to nearest wetland >20 ha; Streams, number of stream inputs/outputs; Swamp, % of wetland that is swamp; Marsh, % of wetland that is marsh; Fen, % of wetland that is fen; Bog, % of wetland that is bog; PW, proportion wetlands within 3000 m; FC, forest cover within 3000 m; Lks, proportion lakes/rivers within 3000 m; 4-L, four-lane highways within 3000 m; TH, total highways within 3000 m; TCR, total centreline roads within 3000 m; Build, building density within 3000 m; Crop, proportion cropped land within 4000 m; Fert, fertiliser applied/hectare within 4000 m; Chem, chemicals applied/hectare within 4000 m; MnTKN, mean total Kjeldahl nitrogen (H_2O); MxTKN, maximum total Kjeldahl nitrogen (H_2O); MinTKN, minimum total Kjeldahl nitrogen (H_2O); MnTP, mean total phosphorus (H_2O); MxTP, maximum total phosphorus (H_2O); MinTP, minimum total phosphorus (H_2O); MnTEP, mean total extractable phosphorus (soil); MxTEP, maximum total extractable phosphorus (soil); MinTEP, minimum total extractable phosphorus (soil); $MnNH_4$, mean ammonium (soil); $MxNH_4$, maximum ammonium (soil); $MinNH_4$, minimum ammonium (soil); $MnNO_3$, mean nitrates (soil); $MxNO_3$, maximum nitrates (soil); $MinNO_3$, minimum nitrates (soil); MnK, mean potassium (soil); MxK, maximum potassium (soil); MinK, minimum potassium (soil); MnMg, mean magnesium (soil); MxMg, maximum magnesium (soil); MinMg, minimum magnesium (soil); MnpH, mean pH (soil); MxpH, maximum pH (soil); MinpH, minimum pH (soil).



ables (Fig. 3). The strongest positive bivariate relationships were with wetland area, proportion wetland, and forest cover, whereas the strongest negative relationships were with total centerline roads and total roads (Fig. 3). The magnitude of the correlations of these variables generally attained a maximum between 2000 and 3000 m (Fig. 4). Although there is a clear tendency for amphibian species richness to decline as the intensity of adjacent land-use increases, inferences about causal relationships are confounded in part by multicollinearity among predictor variables. For example, there is a reasonably strong positive correlation between proportion wetland within 3000 m ($PW_{3000\ m}$) and forest cover within 3000 m ($FC_{3000\ m}$) ($r = 0.46$) and even stronger negative correlations between forest cover and several of the road density variables (e.g., total centerline roads within 3000 m ($TCR_{3000\ m}$); $r = -0.66$).

Multiple regression analysis indicates that the land uses most strongly correlated with amphibian species richness are forest cover, proportion wetlands, and road density: the final selected model explaining the largest proportion (40.5%) of the variance in amphibian species richness included wetland area, $FC_{3000\ m}$, and $PW_{2250\ m}$ (Table 1). Some caution should be used in interpreting the proportion wetland effect: the statistical significance of this relationship is due to a single wetland (Dwyer Hill) that had an unusually high proportion of wetland in its vicinity and unusually high species richness for its size and forest cover. When Dwyer Hill was excluded from the analysis, the effect of wetlands on adjacent lands, although still positive, was no longer statistically significant. All other variables having statistically significant bivariate were no longer significant when included in the multiple regressions with forest cover.

Nutrients

Nitrogen and phosphorus values ranged from 0.34 to 11.20 $mg \cdot L^{-1}$ and from 0.01 to 1.70 $mg \cdot L^{-1}$, respectively. In general, amphibian species richness was more strongly correlated with water nutrient levels than with soil nutrient levels (Fig. 3). Species richness showed statistically significant bivariate negative correlations with maximum and mean TKN (range = 0.68–11.15 and 0.61–5.15 $mg \cdot L^{-1}$, respectively) and maximum, minimum, and mean TP (range = 0.03–1.70, 0.01–0.40, and 0.02–0.68, respectively). Species richness was more highly correlated with mean and maximum values of TKN ($r =$

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–0.40 and –0.44, respectively) and TP (r = –0.45 and –0.46, respectively) than with minimum values (r = –0.16 and –0.26, respectively). Species richness was also significantly correlated with minimum total extractable phosphorus, but the correlations between amphibian species richness and mean and maximum total extractable P and mean K were weak and statistically nonsignificant.

Land use and nutrients

Maximum TKN was the only retained nutrient variable when included in a multiple regression with wetland area, $PW_{2250\ m}$, and $FC_{3000\ m}$; the resulting model explained 42.3% of the variation in amphibian species richness (Table 1; Fig. 5). Maximum TKN was also retained in a model including wetland area, $PW_{2250\ m}$, and $TCR_{2000\ m}$ (Table 1; Fig. 5). In a multiple regression model containing wetland area, proportion wetland, maximum TKN, $TCR_{2000\ m}$, and $FC_{3000\ m}$, neither $FC_{3000\ m}$ nor $TCR_{2000\ m}$ is statistically significant because of the strong correlation between forest cover and total centerline roads. This makes causal inferences difficult, if not impossible. Although it might seem reasonable to select forest cover as the more important correlate because of its larger standardized regression coefficient and stronger bivariate relationship (Fig. 3), if a single wetland (OK Kee Lee) having large leverage is removed from the model, total centerline road has a much larger standardized regression coefficient than forest cover and, in fact, is statistically significant, whereas forest cover is not (Table 1).

Amphibian abundance

There were significant bivariate relationships between amphibian abundance and several land-use and nutrient variables (Fig. 6). A multiple regression model including % $FC_{1750\ m}$, distance to nearest wetland >20 ha ($D_{>20\ ha}$), and $TCR_{200\ m}$ explained 24% of the variation in amphibian abundance (abundance = $0.46(0.42) + 0.97(0.27)FC_{1750\ m} - 0.28(0.14)TCR_{200\ m} + 0.19(0.10)D_{>20\ ha}$; p = <0.001, 0.020, 0.080 for $FC_{1750\ m}$, $TCR_{200\ m}$, and $D_{>20\ ha}$, respectively). However, when pond permanence is included as a categorical variable, the effect of total centerline road is no longer statistically significant (p = 0.099), and a regression with pond permanence, $FC_{1750\ m}$, and $D_{>20\ ha}$ explains 39.1% of the variation in amphibian abundance. If the analysis is done on temporary and permanent ponds separately, the effect of roads is nearly twice as great in the former (β_t = 0.30) as in the latter ponds (β_p = 0.12), although because of low power, neither effect is statistically significant.

Redundancy analyses

We used seven land-use and six nutrient variables in RDA to ordinate amphibian species. The land-use variables were four-lane roads within 3000 m, total highways within 3000 m, $TCR_{3000\ m}$, gravel roads within 3000 m, $FC_{3000\ m}$, $PW_{3000\ m}$, and building density within 3000 m, and the nutrient variables were mean, minimum, and maximum TKN and mean, minimum and maximum TP.

Land use and nutrients explained 17.2% of the variation in species occurrence. The first RDA axis has large negative loadings on $PW_{3000\ m}$ (–0.70) and % $FC_{3000\ m}$ (–0.74), whereas the second axis has large positive loadings on minimum (0.63) and mean TKN (0.59). Again, axis 1 appears to be a general measure of land-use intensity on adjacent lands, whereas axis 2 is a measure of TKN levels independent of adjacent land uses. Ten of the 13 species are positively associated with forest cover and proportion wetland; the exceptions are *R. catesbeiana*, *B. americanus*, and *A. laterale*. Here, *R. catesbeiana* and *R. clamitans* do not show an association with land-use intensity but do have a strong negative association with TKN levels, whereas *B. americanus* is positively associated with land-use intensity and nutrient levels (Fig. 7).

Species presence/absence

Wetland characteristics

The presence of permanent ponds and wetland type are important correlates of presence/absence for several amphibian species. *Rana septentrionalis* (χ^2 = 4.61, p = 0.032, 13 of 62 permanent ponds : 0 of 13 temporary ponds), *R. clamitans* (χ^2 = 9.12, p = 0.003, 55 of 62 permanent ponds : 7 of 13 temporary ponds), and *R. pipiens* (χ^2 = 19.83, p = < 0.001, 61 of 62 permanent ponds : 8 of 13 temporary ponds) showed a statistically significant bivariate relationship with the presence of permanent ponds. *Rana catesbeiana* (17 of 62 permanent ponds : 1 of 13 temporary ponds) and *A. laterale* (13 of 62 permanent ponds : 1 of 13 temporary ponds), while not showing a statistically significant relationship, showed a strong tendency towards wetlands with permanent ponds. All of these species are either strictly aquatic or metamorphose late in the season and require standing water until late summer.

Rana catesbeiana, *R. pipiens*, and *R. clamitans* showed significant associations with predominately marsh habitat, whereas *R. sylvatica*, *A. maculatum*, and *P. crucifer* showed a positive association with swamps.

Land use

Most species show a positive effect of extensive forest cover on adjacent lands at varying distances from the wetland edge, with *R. septentrionalis*, *R. clamitans*, *R. sylvatica*, *H. versicolor*, *A. maculatum*, and *P. crucifer* all having statistically significant positive forest effects. The only species showing a significant negative effect of forest cover (at 100 m) is *R. catesbeiana*. *Rana pipiens* shows a negative effect of $FC_{100\ m}$, but at distances farther from the wetland, forest cover has a small positive effect on *R. pipiens* occurrence (Fig. 8). *Rana septentrionalis*, *R. clamitans*, *R. sylvatica*, *H. versicolor*, and *P. crucifer* are sensitive to high road densities. *Ambystoma laterale*, which had a relatively small (and statistically nonsignificant) positive correlation with forest cover, showed a strong and statistically significant negative correlation with road density at 250 and 1250 m (Fig. 8).

Most species also show a strong positive effect of proportion wetlands at 750 and 3000 m, although the effect is generally much stronger at 3000 m. Those species showing the strongest effect of a high proportion wetlands on adjacent lands are *R. septrentrionalis*, *H. versicolor*, and *R. sylvatica* and, to a lesser extent, *P. crucifer*, *R. pipiens*, and *A. maculatum*. Again, the two species that show a negative effect of proportion wetlands are *R. catesbeiana* and *B. americanus* (Fig. 8).

Nutrients

All species except *B. americanus* were negatively correlated with water nutrient levels. The relationship appears

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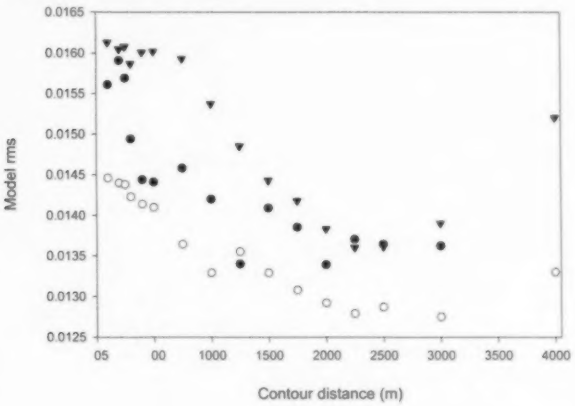
Fig. 4. Plot of model fit (residual mean squares, rms) of the regression models against contour distance; $ASR = a + b_1A + b_2FC_i + b_3PW_j + b_4TCR_k + b_5MaxTKN$, where ASR is amphibian species richness, A is wetland area, FC is forest cover (○), PW is proportion wetlands (▼), TCR is total centreline roads (●), MaxTKN is maximum total Kjeldahl nitrogen, i, j, and k represent contour distances (100 m, 200 m,..., 4000 m), and a, b_1, b_2, b_3, b_4, and b_5 are fitted coefficients. Wetland area and MaxTKN do not change with contour distance so they have not been presented in the figure.



somewhat stronger for nitrogen than phosphorus. All ranid species show a significant negative relationship with early, mean, and (or) maximum TKN levels, as does *P. triseriata*. *Ambystoma maculatum* and *N. viridescens* also show strong, if not statistically significant, negative relationships with TKN (Fig. 8). Most species show similar, if somewhat weaker, relationships with TP. The one exception is *R. catesbeiana*, which shows a strong and statistically significant relationship with early TKN levels but little or no negative correlation with TP.

Most species occurrences also show a negative relationship with soil P levels, but only *R. sylvatica* shows a statistically significant negative relationship. *Bufo americanus* has a statistically significant positive relationship with soil P levels.

Discussion

Species richness

We found a relatively weak positive relationship (relative to species–area relationships for other taxa) between wetland area and species richness, which is consistent with most previous studies of amphibian communities (Findlay and Houlahan 1997; Snodgrass et al. 2000; for an exception, see Vallan 2000). Amphibian richness also showed a positive relationship with forest cover on adjacent lands. Most of the research on deforestation effects has been done on forest-dwelling amphibians (e.g., *Plethodon* spp.) (Petranka et al. 1994; Aubry 2000), although there are recent studies on the correlation between forest cover on adjacent lands and amphibian abundance and (or) species richness in wetland communities (Hecnar and M'Closkey 1998; Kolozsvary and Swihart 1999; Lehtinen et al. 1999). Our results are consistent with the general pattern of positive effects of forest cover (Gibbs 1998*a*; Kolozsvary and Swihart 1999; Lehtinen et al. 1999) generally, and in southern Ontario in particular. Hecnar and M'Closkey (1998) identified forest cover within 2 km (the maximum distance for which data were available) as the most important correlate of amphibian species richness in southwestern Ontario wetlands; our study suggests that these effects extend out to 3 km in southeastern Ontario. These results are also similar to those of Findlay and Houlahan (1997), who reported a positive relationship between herpetofaunal species richness and forest cover extending out to at least 2000 m for a different set of wetlands in southeastern Ontario.

There are several possible explanations for the observed effect of forest cover. First, many surveyed species rely on forests for nonbreeding habitat. *Rana sylvatica*, *P. crucifer*, *H. versicolor*, and the ambystomatids prefer forested habitat to overwinter, and other species such as *N. viridescens* are often found in forests. For these species, the observed relationship may simply reflect loss of necessary habitat. Alternatively, many amphibian species (Sjogren-Gulve 1994; Semlitsch 2000; Joly et al. 2001) exhibit what appears to be metapopulation dynamics, that is, population dynamics characterised by relatively frequent local extinctions and colonisations. For these species, lack of forest cover may impede movement between wetlands, even for species that do not have strong forest requirements, because of greater vulnerability to predation and (or) dessication. If lack of, forest cover has significant negative impacts on movement, colonisation rates will decline, as will the proportion of occupied sites.

Another explanation is that forest cover may simply measure the intensity of agricultural land use and, more specifically, the amount of fertilizer and herbicide–pesticide–fungicide runoff. Nitrates have been implicated in amphibian mortality (Hecnar 1995; Adolfo et al. 1999), as have certain herbicides, fungicides, and pesticides (Dial et al. 1995; Bridges 2000; Bridges and Semlitsch 2000). In fact, four of the species identified in our surveys (*R. clamitans*, *R. pipiens*, *B. americanus*, and *P. triseriata*) have been used in laboratory experiments to evaluate the effects of exposure to ammonium nitrate fertilizer. Toxic effects were found in all four species at nitrate levels that are commonly found in agricultural areas, with *R. pipiens* and *P. triseriata* being most affected. However, we found no relationship between estimated levels of chemical or fertilizer application and species richness independent of forest cover. This may be because chemical applications have little effect on species richness, but it may also be that our estimates of actual chemical and fertilizer application are poor, or that rates of chemical and fertilizer application on adjacent lands are poorly correlated with actual wetland nutrient loading because of complex interactions with topography and drainage patterns, weather, and farming practices. Finally, a related explanation for the forest effect is that forested buffer zones around wetlands serve as contaminant sinks (Hefting and De Klein 1998; Kuusemets and Ulo 1999) and thus protect amphibian communities from the toxic effects of fertiliser and pesticide applications.

We also found a significant negative bivariate correlation with road density on adjacent lands (particularly all two-lane roads with a center line) on amphibian species richness. There is accumulating evidence that roads discourage dis-

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Table 1. Multiple regression models predicting amphibian species richness (numbers in parentheses are standard errors of regression coefficients), coefficients of determination (R^2), and residual mean squares (rms).

Model	R^2, rms	p values
ASR = 0.47(0.04) + 0.08(0.02)A + 0.19(0.06)$FC_{3000\ m}$ + 0.20(0.10)$PW_{2250\ m}$	0.405, 0.010	<0.001, 0.001, 0.028
ASR = 0.68(0.08) + 0.08(0.02)A − 0.11(0.51) $TCR_{2000\ m}$ + 0.28(0.07)$PW_{2250\ m}$	0.360, 0.011	<0.001, 0.016, 0.004
ASR = 0.54(0.05) + 0.07(0.02)A + 0.16(0.06) $FC_{3000\ m}$ + 0.18(0.10)$PW_{2250\ m}$ − 0.10(0.05)MaxTKN	0.423, 0.010	<0.001, 0.006, 0.040, 0.020
ASR = 0.71(0.07) + 0.07(0.02)A − 0.10(0.05) $TCR_{2000\ m}$ + 0.25(0.10)$PW_{2250\ m}$ − 0.12(0.06)MaxTKN	0.383, 0.010	0.003, 0.020, 0.008, 0.030
ASR = 0.65(0.09) + 0.06(0.02)A + 0.11(0.07) $FC_{3000\ m}$ − 0.06(0.05)$TCR_{2000\ m}$ + 0.19(0.10) $PW_{2250\ m}$ − 0.11(0.05)MaxTKN	0.430, 0.010	0.003, 0.054, 0.083, 0.036, 0.016
ASR = 0.68(0.10) + 0.06(0.02)A + 0.09(0.07) $FC_{3000\ m}$ − 0.08(0.05)$TCR_{2000\ m}$ + 0.22(0.10) $PW_{2250\ m}$ − 0.13(0.05)MaxTKN	0.434, 0.009	0.003, 0.100, 0.048, 0.024, 0.008

Note: ASR, amphibian species richness; $FC_{3000\ m}$, forest cover within 3000 m; $PW_{2250\ m}$, wetland density within 2250 m; $TCR_{2000\ m}$, total centreline roads within 2000 m; A, wetland area; MaxTKN, maximum total Kjeldahl nitrogen.

*This model has had one wetland removed to illustrate how the relative importance of road density vs. forest cover is dependent on a single wetland.

persal (Gibbs 1998*b*; deMaynadier and Hunter 2000), increase mortality (Fahrig et al. 1995; Hels and Buchwald 2001), and reduce genetic diversity (Reh and Seitz 1990) of amphibians. Any or all of these may lead to declines in amphibian species richness and would explain the correlation of road density with diminished amphibian species richness (Findlay and Houlahan 1997; Vos and Chardon 1998; Lehtinen et al. 1999).

When both road density and forest cover are included in multiple regression models along with wetland area, proportion wetland, and nutrient levels, neither variable shows a statistically significant correlation with species richness. In a large part, this is due to a strong negative correlation between road density and forest cover in our sample. This result is similar to earlier findings (Findlay and Houlahan 1997), except that in that sample of wetlands, the correlation of roads with amphibian species richness was stronger than forest cover, whereas here the situation is reversed.

The strong correlation between road density and forest cover makes interpretation of the relative importance of their effects difficult. It is possible, for example, that only one has a causal relationship with species richness, with the other relationship being simply an artefact of the road – forest cover relationship. This seems unlikely, however, because when both are included in the statistical model, both show near-significant correlations. What is required are predictor variables that can begin to tease apart the independent or joint effects of these two variables. For example, recent research indicates that amphibian mortality increases exponentially with traffic volume (Hels and Buchwald 2001), and so the issue may be clarified if traffic volume data were available. Identification of improved measures of the possible effects of roads will be a subject of future research.

We also showed a positive relationship between amphibian species richness and the proportion of adjacent land area that is itself wetland. Metapopulation theory predicts that isolated wetlands will have lower amphibian species richness because of (*i*) decreased likelihood of recolonisation following local extinction and (*ii*) lower frequency of "rescue" events (i.e., immigration from outside sources that prevent local extinctions). There is clear evidence that amphibian species richness and (or) the distribution of specific species correlates with wetland isolation (Sjogren 1991; Sjogren-Gulve 1994; Skelly et al. 1999) and that immigration rates increase and extinction rates decrease with proximity to neighboring ponds. These studies measured proximity by the distance to the nearest wetland, a variable that did not show any significant associations with species richness in the present study. However, it may be that the proportion of adjacent area in wetland habitat is as or more important than proximity alone (Gibbs 2000; Semlitsch 2000). A second explanation for the effect of neighbouring wetlands is that they ameliorate the negative impacts associated with fertilizer, pesticide, and herbicide applications by serving as sinks for pollutants (Moore et al. 2000; Schulz and Peall 2001).

Amphibian species richness was also negatively correlated with water TKN levels independent of other variables, with the strongest relationships observed with maximum TKN levels. This is consistent with experimental results showing that elevated nitrite and nitrate levels (i.e., above some threshold) induce significant mortality in many amphibian species (Hecnar 1995; Watt and Jarvis 1997; Adolfo et al. 1999). But hitherto, there has been virtually no evidence from field studies, experimental or epidemiologica, of nitrogen effects on amphibian communities (Hecnar and M'Closkey 1996).

Amphibian abundance

Landscape-scale studies of aquatic breeding amphibian density are relatively rare, but the few existing studies have shown positive relationships with increasing water levels in ephemeral ponds (Nyberg and Lerner 2000), amount of mixed hardwood forests (Mitchell et al. 1997; Waldick et al. 1999; Hanlin et al. 2000) on adjacent lands, size of forested buffer strips (Dupuis and Steventon 1999), and hydroperiod (Pechmann et al. 1989; but see Babbitt and Tanner 2000) and negatively associated with wetland area (Vallan 2000; but see Babbitt and Tanner 2000), urban development (Delis et al. 1996), and roads (Fahrig et al. 1995). We found positive correlations of forest cover, distance to large neighboring wetlands, amount of marsh, and presence of permanent ponds and negative correlations of road density, consistent with many of these previous studies. Our abundance values are primarily an index of the abundance of large ranid species, primarily *R. pipiens* and *R. clamitans* and to a lesser

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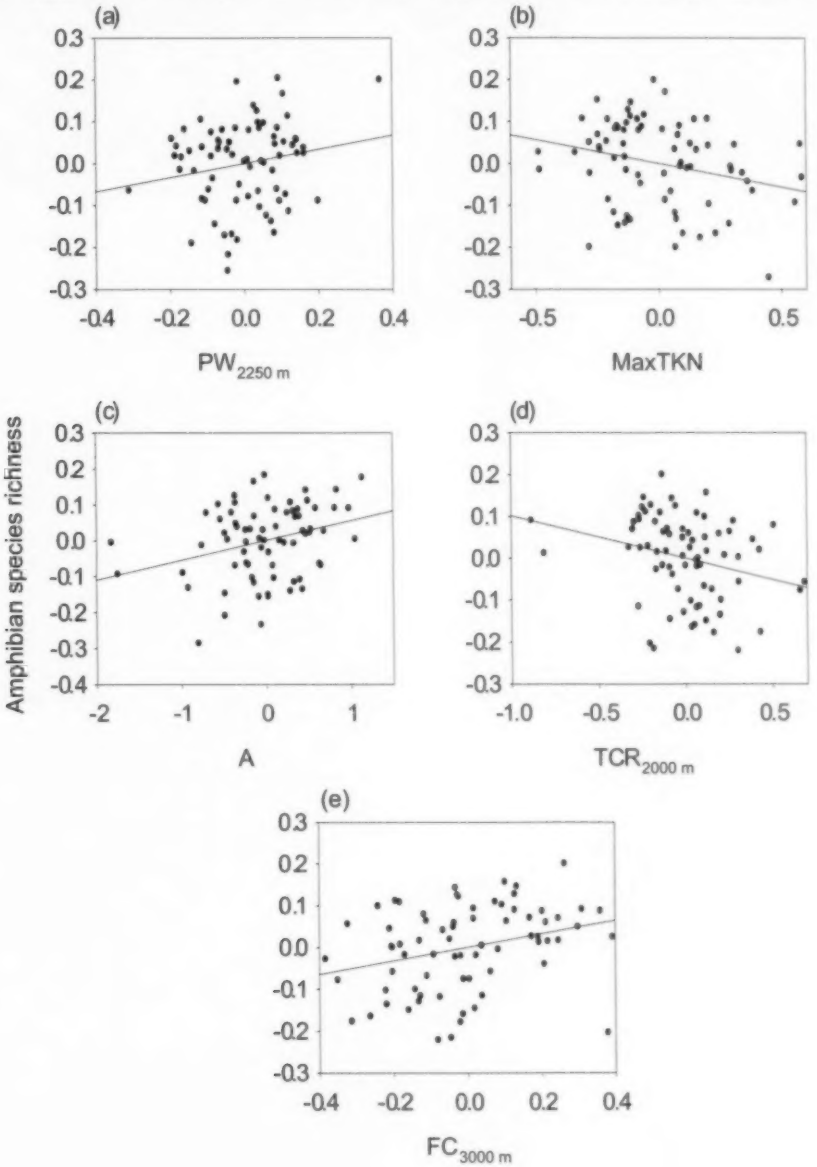
Fig. 5. Partial–partial plots of the relationships between amphibian species richness and (*a*) proportion wetland within 2250 m ($PW_{2250\ m}$), (*b*) maximum total Kjeldahl nitrogen (MaxTKN), (*c*) wetland area (*A*), (*d*) total centreline roads within 2000 m ($TCR_{2000\ m}$), and (*e*) forest cover within 3000 m ($FC_{3000\ m}$). The relationships are controlled for other significant variables in multiple regression models.



degree *R. septentrionalis* and *R. catesbeiana*. All of these species generally overwinter in ponds and often do not metamorphose until their second summer. Consequently, we would expect lower abundances of these species in wetlands without permanent standing water. This effect might not be as strong if abundance of species that overwinter terrestrially (e.g., *P. crucifer* and *R. sylvatica*) were better represented in our measure of amphibian abundance. These aquatic species are usually associated with emergent nonwoody vegetation and open water, so again, it is not surprising that they are more abundant in wetlands that have relatively more marsh than swamp, fen, or bog.

Amphibian abundance is also positively correlated with forest cover on adjacent lands. Neither *R. pipiens* nor *R. clamitans* are thought to have strong requirements for forested habitat (although in the present study, we found *R. clamitans* presence positively correlated with surrounding forest cover), so that forest cover may simply index wetland water quality (e.g., pesticide and (or) nitrate concentrations are lower in wetlands with more forest around them).

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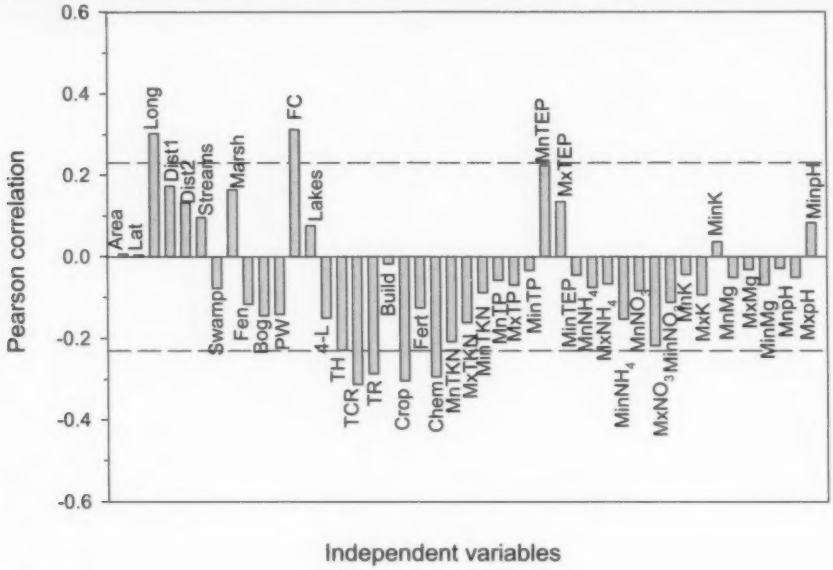
Fig. 6. Correlation coefficients for all independent variables used in amphibian abundance regression analyses. The upper and lower broken lines indicate statistical significance at $\alpha = 0.05$. The independent variable key is the same as for Fig. 3.



In contrast to amphibian species richness, amphibian abundance showed a significant negative correlation with road density on adjacent lands that was independent of forest cover and was largest within 100 m of the wetland edge. Moreover, the effect size of road density within 100 m is twice as large for wetlands without permanent standing water compared with those with permanent standing water. The results are consistent with the hypothesis that the road effect arises from increased mortality during movement between wetlands and to or from adjacent habitats. *Rana clamitans* and *R. pipiens* in eastern Ontario often overwinter in ponds with permanent standing water and therefore must migrate from wetlands without permanent ponds, thereby exposing themselves to increased risk from road mortality. The impetus to disperse across roads is not likely as great in wetlands already containing permanent standing water. Indeed, we suspect that the road effect would be even stronger if species that move from terrestrial habitats to breeding sites were better represented in the amphibian abundance index.

Community composition

Most amphibian species in southeastern Ontario wetlands are, to a greater or lesser degree, associated with low land-use intensity on adjacent lands (i.e., high forest cover and proportion wetland and low road density). Species such as *H. versicolor*, *R. sylvatica*, *P. triseriata*, *A. maculatum*, and *P. crucifer* that use forested areas to overwinter and (or) must migrate between breeding areas and overwintering areas show a strong association with wetlands surrounded by extensive forest cover and low road densities. It is a little more surprising that an aquatic hibernator not known to use forested habitat extensively such as *R. septentrionalis* shows at least as strong an association. Possibly *R. septentrionalis* populations have strong metapopulation dynamics and, as such, require low-intensity land use on adjacent lands to maintain migration rates. The two species that show an association with intensive land use are *B. americanus* and *R. catesbeiana*. *Bufo americanus* is common in highly fragmented and human-modified environments (Kolozsvary and Swihart 1999; Lehtinen et al. 1999; Waldick et al. 1999). *Bufo americanus* is known to prefer shallow, warm waters for breeding, and those habitats may be more common in human-modified landscapes. It is also possible that *B. americanus* is present at these sites because they are able to avoid competition with and (or) predation by more sensitive species. *Bufo americanus* has a very short larval stage; larvae are very small and are, at least in some circumstances, competitively inferior to larger ranid species (Alford 1989, but see Alford and Wilbur 1985). They are also known prey for other amphibian species (Morin 1983; Alford 1989; Wilbur and Fauth 1990). *Rana catesbeiana* are generally considered to be good competitors (Werner 1994; Kupferberg 1997), so it seems unlikely that their presence in intensively modified landscapes is a consequence of competitive displacement by other species in more intact landscapes. Because they do not generally disperse from their breeding ponds, they may be less affected by forest loss–conversion and road mortality than other species and, hence, are more likely to occur in wetlands in heavily modified landscapes.

Although most amphibian species showed increased probability of occurrence at wetlands with lower nutrient status, for only two (*R. clamitans* and *R. catesbeiana*) was this effect independent of other habitat considerations. These species are almost exclusively aquatic and often overwinter in the larval stage and hence will have the highest exposure to stressors in the aquatic environment. The fact that these two species are the most sensitive to elevated nutrient levels sug-

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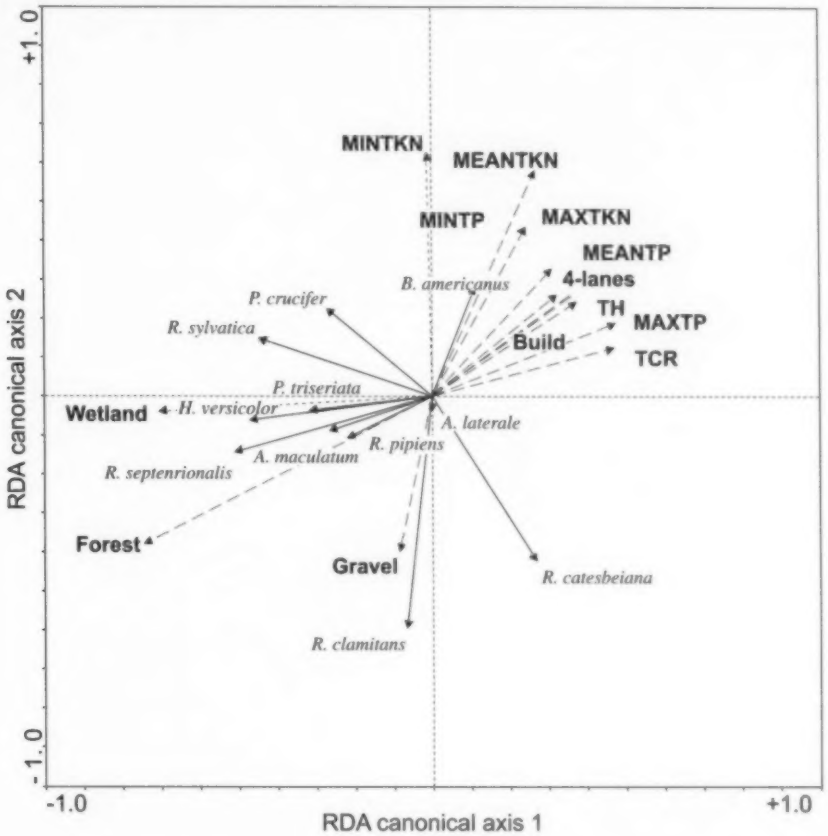
Fig. 7. Redundancy analysis (RDA) ordination biplot: presence/ absence of 11 amphibian species at 75 wetland sites against land-use and nutrient variables (four-lane roads within 3000 m (4-lanes), total highways within 3000 m (TH), total centerline roads within 3000 m (TCR), gravel roads within 3000 m (Gravel), forest cover within 3000 m (Forest), proportion wetland within 3000 m (Wetland), building density within 3000 m (Build), mean, minimum, and maximum total Kjeldahl nitrogen (MEANTKN, MINTKN, and MAXTKN, respectively), and mean, minimum, and maximum total phosphorus (MEANTP, MINTP, and MAXTP, respectively)).



gests that this relationship is not just an artefact of the correlation between nutrient levels and other land-use variables in our survey.

Individual species occurrence

Several species showed an association with wetlands with permanent ponds (*R. septentrionalis*, *R. clamitans*, *A. laterale*, and *R. catesbeiana*), including *R. pipiens*, which in our survey was associated with permanent ponds, despite having been previously identified as a species that prefers temporary ponds (Hine et al. 1981). Nonetheless, *R. pipiens* was often found in wetlands without permanent ponds (6/13) unlike the other species (except *R. clamitans*; 7/13) that were rarely if ever found in such conditions.

Forest cover was a significant predictor of the presence of several species (*R. septentrionalis*, *R. sylvatica*, *R. clamitans*, *H. versicolor*, and *A. maculatum*). It is notable, however, that the spatial scale of the effect of forest cover varied substantially among species, with *R. septentrionalis*, *R. clamitans*, and *H. versicolor* showing the strongest correlation at 3000–4000 m, *R. sylvatica* and *A. maculatum* at 100 m. One explanation is that forest cover at larger scales is a generalized indicator of a number of different anthropogenic stressors (e.g., road density, nutrient loading, etc.), each of which may exert different causal effects, whereas forest cover at smaller scales is primarily a measure of habitat availability. In our sample of wetlands, forest cover at 3000 m is more highly correlated with road density and nutrient levels in both soil and water than forest cover at 100 m (J. Houlahan, unpublished data), suggesting that the former is indeed a general index of anthropogenic stress.

Alternatively, the difference in the geographical scale of the forest cover relationship among species may be an effect of different dispersal patterns. *Rana sylvatica* has been shown to be highly philopatric to natal breeding ponds (Berven and Grudzien 1990), and most ambystomatids rarely disperse over long distances. Such species may well use forest habitat in close proximity to wetland breeding sites. By contrast, *R. clamitans* is known to move relatively large distances (up to 2 km) from breeding sites (Lamoureux and Madison 1999). The magnitude of the effects of forest cover follow approximately the order that we would expect, with species that re-

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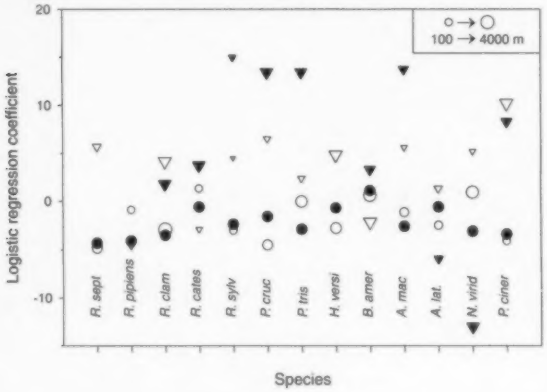
Fig. 8. Bivariate logistic regression coefficients for four important land-use predictors of individual species presence/absence (forest cover within 3000 m (▽), total centreline roads within 1250 m (○), proportion wetland within 3000 m (▼), and maximum total Kjeldahl nitrogen (●)). Symbol size increases with the scale at which land-use variables show the strongest correlations (smallest (100 m) to largest (4000 m)).



quire forest habitat to carry out a portion of their life cycle (e.g., *P. cinereus*, *A. maculatum*, and *R. sylvatica*) showing the strongest correlations compared with those (*R. pipiens*, *B. catesbeiana*, and *B. americanus*) that do not have such requirements.

Many species showed negative bivariate relationships with road density at various distances from the wetland edge, including *R. septentrionalis*, *R. clamitans*, *H. versicolor*, *P. crucifer*, and *A. laterale*. Road density was a significant predictor of occurrence, independent of other confounding variables, for *P. crucifer*, *A. laterale*, and perhaps *R. septentrionalis*. Roads have been found to be a barrier to ambystomatid movement at traffic volumes much lower than that present on most roads in this study (deMaynadier and Hunter 2000). Findlay et al. (2001) show a negative effect of road density, independent of forest cover, on *R. sylvatica* and *R. septentrionalis* and a limiting effect on anuran species richness, but deMaynadier and Hunter did not find an effect on anurans. There is convincing evidence that some ranids experience high levels of road mortality (Herden et al. 1998; Hels and Buchwald 2001), and this may explain the observed negative relationship between surrounding road density and the occurrence of several ranid species (Vos and Chardon 1998) or anuran species richness (Findlay et al. 2001).

Several species showed significant positive relationships with the amount of wetland on adjacent lands (generally with 2000–3000 m of the wetland edge), including *R. septentrionalis*, *R. sylvatica*, *H. versicolor*, and *A. maculatum*, whereas one species (*R. clamitans*) showed a negative relationship. For species with true (or approximate) metapopulation structure, we would expect that the probability of being present at a site is positively related to the number, size, and proximity of neighboring wetlands. Kolozsvary and Swihart (1999) showed that an index that incorporates size, number, and proximity of neighboring wetlands was a better predictor of amphibian species richness in 30 midwestern U.S. forest fragments than neighboring wetland proximity alone. Moreover, there is good evidence that several hylid species (Carlson and Edenhamn 2000), bufonids (Sinsch 1997; Rowe et al. 2000), and ranids (Sjogren-Gulve 1994; Perttu and Laurila 1999) have the high local extinction and recolonisation rates associated with metapopulation structure and that movements of 2–3 km over short periods of time are not unusual (Sinsch 1997). There is less published evidence of metapopulation structure in ambystomatids, although there is evidence that they can disperse relatively long distances (Storfer 1999). Another possible explanation for the positive correlation of increased amounts of wetland on adjacent land with amphibian species richness is that it improves wetland water quality (Weller et al. 1996; Tufford et al. 1998; Bis et al. 2000).

The occurrence of several anurans, including *R. septentrionalis*, *R. clamitans*, *R. catesbeiana*, *R. sylvatica*, and *P. triseriata*, were negatively correlated with water nutrient levels, whereas no urodeles showed a similar pattern. This is consistent with recent research that suggests that salamanders are less sensitive to chronic nitrate exposure than anurans (Adolfo et al. 1999). *Rana septentrionalis* and *R. sylvatica* were less likely to be found at sites with high TKN and (or) high TP values, whereas *R. catesbeiana* and *R. clamitans* were less likely to be found at sites with high TKN values. *Pseudacris triseriata* appeared to be more sensitive to TP levels. The strongest correlations with nutrient levels were for *R. catesbeiana*, *R. septentrionalis*, and *R. clamitans*, aquatic anurans with relatively long larval periods and, hence, comparatively prolonged exposure to stressors in the aquatic environments such as elevated nutrient levels. These species-specific results are consistent with those from the RDA ordinations.

Management implications

Although it is clear that adjacent land use is not the only important factor structuring amphibian communities, our best models explain less than 50% of the variation in species richness and abundance, we conclude that adjacent land uses affect amphibian species richness and community composition through a complex suite of effects, including loss of habitat, diminished dispersal ability, declining water quality, and increased exposure to toxic substances. Thus, despite evidence that the causes of amphibian declines may include factors that operate over large spatial scales (e.g., UV-B exposure), factors like adjacent land use that operate at local and regional scales play a significant role in structuring amphibian communities, and regulation of land use at the local and regional levels will be essential for the conservation of wetland amphibian communities. The obvious question, but one that has received relatively little attention, is at what scale do we need to manage adjacent land use? The scale at which we manage amphibian communities, and indeed any natural community, must reflect the scale at which the important drivers of community composition and species richness work. For amphibians, the scale appears to be quite large with demonstrable effects of increased land-use intensity out to 3000 m for species richness and out to 4000 m for some individual species. This means that the concept of "buffer zones" as a management technique for protecting

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amphibian communities is impractical because the size of an effective buffer zone would be prohibitively large. Effective management of wetland amphibian communities will require managing "communities" of wetlands rather than individual wetlands and land-use planning aimed at maintaining critical threshold levels of forest cover, proportion wetland, and perhaps, road densities or traffic volumes at the regional scale. That said, local management might be effective for species-specific concerns. For instance, there is evidence that the effects of forest cover beyond 100 m on *R. sylvatica* are not important, and therefore local management of forest cover for *R. sylvatica* might be effective.

Current Ontario policy conserves wetlands on an individual basis, places no constraints on agricultural land uses, and regulates adjacent land use out to 120 m, stating that "it is known that developments within 120 meters of wetlands have a reasonable probability of affecting the ecological functions of the wetlands which they surround" (Ontario Ministries of Municipal Affairs and Natural Resources (OMMA and OMNR) 1992). This research adds to a growing mound of evidence that regulation of a 120-m band will not mitigate negative impacts to wetland ecological functions caused by incompatible adjacent land use and, in particular, by incompatible agricultural practices. The policy does state, however, that "the diversity of natural features in an area, and the natural connections between them, should be maintained..." (OMMA and OMNR 1992), and effective wetland conservation management will require that we define the appropriate "diversity of natural features", the size of an "area", and the nature of "natural connections" and regulate land use accordingly.

It is not surprising that, in general, management of wetland amphibian communities must occur at the regional scale given that (*i*) most amphibian species have habitat requirements that extend far beyond the boundaries of an individual wetland, (*ii*) many amphibian species exhibit metapopulation dynamics and, thus, by definition require "communities" of wetlands, and (*iii*) local water quality is often strongly correlated with regional-scale land-use intensity (Hunsaker and Levine 1995; Gangbazo 2000). For wetland conservation to be effective, it is critical that international, national, and (or) provincial/state policies begin to reflect these biological realities.

In conclusion, adjacent land uses have a significant impact on amphibian species richness, abundance, and community composition, with the size and quality of adjacent habitat being at least as important as, if not more important than, the size and quality of the breeding habitat. Incompatible adjacent land uses can affect amphibian species richness and community composition out to 3000–4000 m from the wetland edge. Important correlates of amphibian species richness included forest cover, road density, proportion wetland, wetland size, and water nitrogen levels. The magnitude and direction of land-use and nutrient effects varied widely among species, so important drivers of amphibian communities will often not be identified using only species richness as an end point. Finally, the scale of land-use effects is so large that management of southeastern Ontario wetlands for amphibian species richness must be at the regional rather than local scale.

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Appendix A

Potassium and magnesium

1. Add 25 mL of 1.0 mol/L ammonium acetate extractant to 2.5 cm^3 of prepared soil.
2. Shake for 15 min ensuring that soil is kept in suspension.
3. Filter through a Whatman No. 2 filter paper.
4. Dilute filtrate with distilled water (1:9).
5. Read on atomic absorption spectrophotometer. Potassium is read at 766.5 nm and magnesium at 285.2 nm.

Sodium bicarbonate extractable phosphorous

1. Add 50 mL of 0.5 mol/L sodium bicarbonate extractant to 2.5 cm^3 of prepared soil.
2. Shake for 30 min ensuring that soil is kept in suspension.
3. Filter through a Whatman No. 5 filter paper.
4. Read on colorimetric autoanalyzer.

Note that a series of five standards was used to check calibration on chart, the wavelength of the analysis was 820 nm, and a known sample was included in each tray of 40 samples.

Nitrate and ammonium

1. Add 25 mL of 2.0 mol/L potassium chloride extractant to 5.0 g of soil.
2. Shake for 30 min ensuring that soil is kept in suspension.
3. Filter through a Whatman No. 42 filter paper.
4. Read on colorimetric autoanalyzer.

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Potential impact of forest harvesting on lake chemistry in south-central Ontario at current levels of acid deposition

S.A. Watmough, J. Aherne, and P.J. Dillon

Abstract: The potential impact of harvesting on lake chemistry was assessed for ~1300 lakes in south-central Ontario using a critical loads approach based on the steady-state water chemistry (SSWC) model. The critical load of acidity is currently only exceeded by bulk sulphate deposition in 9% of the lakes if harvesting does not occur. However, the percentage increases to 23%, 56%, and 72% under potential harvesting scenarios that assume wood-only (stem without bark), stem-only, or whole-tree harvesting, respectively. This increase in exceedance of critical load is due to the much lower base cation concentrations in lakes resulting from base cation removals during harvest. For example, only 0.3% of lakes will have Ca^{2+} concentrations <50 μequiv·L^{-1} if harvesting does not occur, whereas 52% of lakes will have Ca^{2+} concentrations <50 μequiv·L^{-1} if whole-tree harvesting occurs. Harvesting clearly has an enormous potential impact on lake chemistry, which will become more apparent as exchangeable base cation pools in soil decline and acid inputs can no longer be buffered.

Résumé : La méthode des charges critiques basée sur le modèle stable de la chimie de l'eau (SSWC) nous a permis de déterminer l'impact potentiel de la récolte forestière sur ~1300 lacs du centre sud de l'Ontario. La charge critique d'acidité est actuellement dépassée par les dépôts bruts de sulfates dans seulement 9 % des lacs, en l'absence de récolte forestière. Cependant, dans les trois scénarios potentiels de récolte suivants, bois seul (troncs sans écorce), troncs seuls et arbres entiers, les pourcentages augmentent respectivement à 23 %, 56 % et 72 %. Cet accroissement du dépassement de la charge critique s'explique par des concentrations beaucoup plus faibles de cations basiques dans les lacs, à cause de leur retrait durant la récolte. Ainsi, seuls 0,3 % des lacs ont des concentrations de Ca^{2+} <50 μequiv·L^{-1} en l'absence de récoltes, alors que 52 % des lacs ont de telles concentrations lorsque les arbres entiers sont récoltés. La récolte forestière a donc un impact potentiel considérable sur la chimie des lacs, ce qui devient plus apparent à mesure que les réserves de cations basiques échangeables du sol diminuent et que les apports d'acides dans les lacs ne sont plus tamponnés.

[Traduit par la Rédaction]

Introduction

Critical load is defined as "a quantitative estimate of an exposure to one or more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge" (Nilsson and Grennfelt 1988). Traditionally, surface water critical load models are used to calculate acceptable levels of sulphate (SO_4^{2-}) deposition to lakes (Henriksen and Posch 2001). The most common method for calculating critical loads of acidity, CL(A), for lakes is the steady-state water chemistry (SSWC) model (Henriksen et al. 1992, 2002; Posch et al. 2001). Presently, however, very few lakes in central Ontario have chemistry similar to that calculated by the SSWC model because soils are rarely at steady state and inputs of base cations to lakes exceed those predicted by the SSWC model because of losses from the exchangeable base cation pool in soil. The SSWC model uses the so-called *F* factor to account for part of the present base cation leaching that results from ion exchange processes in soils (Henriksen and Posch 2001).

During the past 20 years, bulk SO_4^{2-} deposition in south-central Ontario has decreased by approximately 40%, and as a result, the number of lakes that exceed the SSWC CL(A) in various parts of the region has decreased from 74%–82% to 11%–26% (Henriksen et al. 2002). These critical load calculations are based on the estimation of "pre-industrial" base cation inputs and are a reliable indicator of base cation inputs into lakes, but only under conditions that assume no harvesting (Watmough and Dillon 2002). In fact, south-central Ontario is dominated by mixed hardwood forest, much of which is harvested to some extent. For example, in 1998–1999, more than one million cubic metres of timber were harvested in south-central Ontario. It is well established that harvesting can result in the removal of substantial amounts

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of base cations from soil (Johnson et al. 1988), yet accurate estimates of base cation removal during harvest in south-central Ontario are not available. Removal of base cations from soil through harvesting must ultimately result in lower base cation concentrations in lakes, and consequently, lakes surrounded by catchments that are harvested will be more sensitive to acid deposition, i.e., have a lower critical load (Sverdrup and Warfvinge 1990; Helliwell et al. 2001).

The impact of harvesting on lake chemistry will be most pronounced in areas such as south-central Ontario where soils are generally very shallow and have low weathering rates (Dillon et al. 1978). Currently, soils in the region are acidifying and large losses of calcium from the exchangeable pool have occurred during the past 20 years, although base cation losses have decreased in recent years in response to decreased SO_4^{2-} leaching (Watmough and Dillon 2003*b*). Base cation losses from the exchangeable pool are currently buffering lakes to some extent against the adverse impacts of acid deposition, although this is only a temporary phenomenon and ultimately base cation inputs into lakes must decrease as exchangeable base cation pools become depleted. Harvesting will further contribute to the depletion of the base cation pools, and the extent of harvesting will ultimately determine the base cation inputs into lakes. This in turn will determine the sensitivity of lakes to acid deposition. In this study, we calculate the CL(A) and base cation (Ca^{2+}, Mg^{2+}, K^+) concentrations at steady state for more than 1300 lakes in south-central Ontario using the SSWC model. Calculations were performed assuming wood-only (stem without bark), stem-only, and whole-tree harvesting scenarios, applied to all lakes, in an attempt to gauge the potential impact of harvesting on lake chemistry in the region.

Materials and methods

Study region

The chemistry of freshwaters in central Ontario is related in general terms by their location relative to the boundary of the Precambrian Shield. All of the lakes in this study are situated on the Precambrian Shield; a region of predominately silicate bedrock, which is overlain by thin glacial tills. There are many localised exceptions, but the bedrock and surficial geology of this region results in lakes and streams that contain soft waters (conductivity typically ranges between 15 and 40 $\mu S \cdot cm^{-1}$) that are low in nutrients as well as major ions. Many contain appreciable levels of dissolved organic carbon (DOC), and organic anions often form a major component of the charge balance.

The climate of the study area is north temperate, with long-term average precipitation ranging between ca. 800 and 1100 mm, about one-quarter to one-third of which falls as snow. The mean monthly temperature ranges between –5 and –10 °C in the coldest winter months and between 22 and 25 °C in the summer.

The study area lies within the Great Lakes – St. Lawrence region of Ontario and is dominated by seminatural mixed hardwood forests. Sugar maple (*Acer saccharum*) dominated forest stands dominate much of the landscape, especially in the eastern section, although white pine (*Pinus strobus*) is dominant in some areas. Associated tree species include American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), yellow birch (*Betula allegheniensis*), white ash (*Fraxinus americana*), basswood (*Tilia americana*), ironwood (*Ostrya virginiana*), red pine (*Pinus resinosa*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), hemlock (*Tsuga canadensis*), aspen (*Populus* sp.), and white birch (*Betula papyrifera*). Small wetlands dominated by white cedar (*Thuja occidentalis*) and black spruce (*Picea mariana*) are ubiquitous throughout the entire region, covering an estimated 10% of the total area.

This region was heavily logged in the late 1800s, initially for white pine, but later other tree species were targeted by loggers. Forests are generally unevenly aged, their composition and age structure determined largely by forest management practices. In this region, about 60% of the harvesting is by selective cutting, 30% by shelterwood, and 10% is clearcut. For example, during selection management, small groups of trees or individual trees of varying sizes are removed at regular (~15 years) intervals depending on the management plan. This process favours shade-tolerant species such as sugar maple, and forest regeneration is usually through natural processes. In contrast, clearcuts favour shade-intolerant species, and sometimes regeneration is initiated through artificial planting. There are also many regions in which no harvesting occurs.

Lakes in the current study are situated in the District of Muskoka or the counties of Haliburton, Nipissing, and Parry Sound in south-central Ontario (Fig. 1). Forest type, soils, geology, and deposition are relatively uniform within the entire study region, and most lakes in this region are sensitive to the deposition of strong acids because of their geological setting on the Precambrian Shield (Dillon et al. 1978).

Critical load calculations

The SSWC model has been described in detail by a number of authors (Sverdrup et al. 1990; Werner and Spranger 1996; Henriksen and Posch 2001). Briefly, the model uses current base cation concentrations in lakes and the *F* factor to estimate base cation inputs in pre-industrial times. The pre-industrial base cation input determines the critical load of the lake. The current application follows the most recently published description (Henriksen and Posch 2001; Henriksen et al. 2002); the critical load of acidity for surface waters (expressed as an annual flux, $meq\text{uiv} \cdot m^{-2} \cdot year^{-1}$) is calculated as follows:

$$(1) \quad CL(A) = Q([BC]_0 - [ANC]_{limit})$$

where Q is the mean annual runoff ($m \cdot year^{-1}$), $[BC]_0$ is the pre-acidification base cation ($BC = Ca^{2+} + Mg^{2+} + K^+ + Na^+$) concentration in lake water, and $[ANC]_{limit}$ is the preselected damage-threshold level for sensitive indicator organisms. In this study, an $[ANC]_{limit}$ of 40 $\mu equiv \cdot L^{-1}$ was chosen to match that used by Henriksen et al. (2002) for 1469 lakes in south-central Ontario. $[BC]_0$ is estimated from the present base cation concentration minus the long-term changes in base cation concentration, inferred from the inputs of strong acid anions through the *F* factor:

$$(2) \quad [BC]_0 = [BC]_t - F([SO_4^{2-}]_t + [NO_3^-]_t - [SO_4^{2-}]_0 - [NO_3^-]_0)$$

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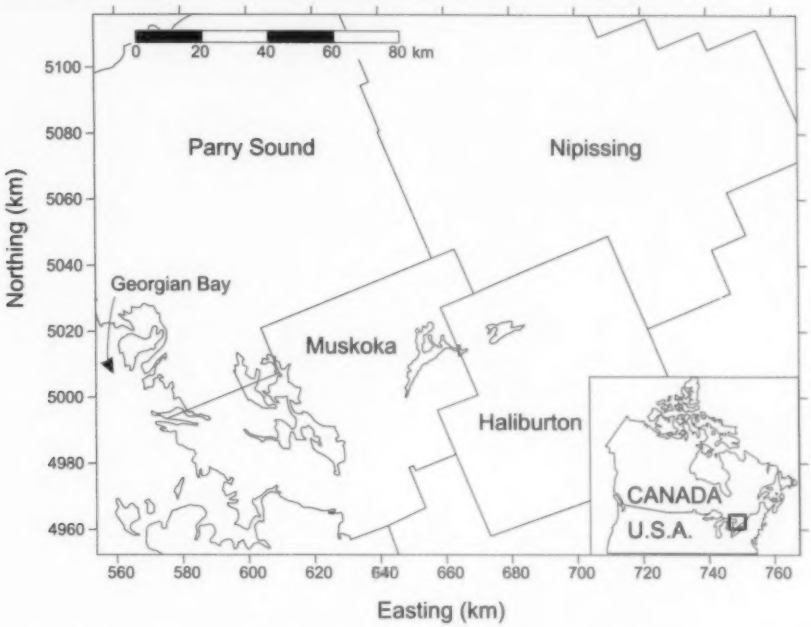
Fig. 1. Location of the study region (Muskoka, Haliburton, Nipissing, and Parry Sound regions shown) in south-central Ontario, Canada (co-ordinate projection: World Geodetic System 1984, Universal Transverse Mercator Zone 17N).



where the subscripts 0 and t refer to pre-acidification and present concentrations, respectively. The F factor represents the fraction of present base cations due to soil acidification:

$$(3) \qquad F = \sin\left(\frac{(\pi/2)Q[\mathrm{BC}]_t}{S}\right)$$

where S is the base cation flux at which $F = 1$. For Norway, S has been estimated to be 400 mequiv.·m^{-2}·year^{-1}. If $Q[\mathrm{BC}]_t >$ 400, then F is set to 1.

$[SO_4^{2-}]_0$ is estimated from the relationship between $[SO_4^{2-}]_t$ and $[\mathrm{BC}]_t$ for lakes in regions little affected by acid, and $[NO_3^-]_0$ is assumed to be zero. For Norway, the following relationship exists (Henriksen and Posch 2001):

$$(4) \qquad [SO_4^{2-}]_0 = 8 + 0.17[\mathrm{BC}]_t$$

This equation suggests that there is an atmospheric background contribution of $[SO_4^{2-}]$ equal to 8 μequiv.·L^{-1} and a geological contribution proportional to the concentration of base cations. Equations 3 and 4 have previously been deemed appropriate for south-central Ontario (Henriksen and Dillon 2001; Henriksen et al. 2002).

Finally, the exceedance of sulphur acidity, Ex(A), is calculated as the long-term deposition flux of non-seasalt SO_4^{2-} (S_{dep}) minus critical load (negative exceedances are "not exceeded"):

$$(5) \qquad \mathrm{Ex(A)} = S_{dep} - \mathrm{CL(A)}$$

The present exceedance of critical load may also be defined by inclusion of nitrogen leaching in the exceedance calculations (see Henriksen and Posch 2001). However, this has not been carried out in the current study, as nitrogen concentration data are not available for all lakes.

According to the SSWC model, $[\mathrm{BC}]_0$ calculated using current lake chemistry and the F factor should include an estimate of base cation uptake by trees (Henriksen et al. 1992). However, Watmough and Dillon (2002) demonstrated that the SSWC model is a reliable indicator of base cation inputs into lakes in central Ontario under conditions that assume no harvesting. Indeed, Henriksen and Posch (2001) stated that "if there is a change in the net uptake due to changes in management practices (i.e., forest harvesting), this has to be taken into account". Therefore, the impact of harvesting should be considered in the critical load calculations for lakes, although in practice it is rarely done, primarily because of the ambiguity regarding how harvest removals should be treated in the SSWC model. As such, exceedance of the CL(A) can be calculated as follows (Henriksen and Posch 2001):

$$(6) \qquad \mathrm{Ex(A)} = S_{dep} - \mathrm{CL(A)} + \mathrm{BC}_{up}$$

where BC_{up} is the net base cation removal through harvesting (note that BC in this instance is only $Ca^{2+} + Mg^{2+} + K^+$ as Na^+ concentrations in vegetation are low and are not included in base cation uptake estimates in critical load calculations). Estimates of harvesting removal vary depending on forest type, harvesting practice, and forest age.

Concentrations of Ca^{2+}, Mg^{2+}, and K^+ that exist in lakes at steady state under the various harvesting scenarios were calculated using eq. 2. However, pre-industrial concentration was calculated separately for $[Ca^{2+}]_0$, $[Mg^{2+}]_0$, and $[K^+]_0$, rather than $[\mathrm{BC}]_0$, and the individual base cation removals resulting from harvesting were subtracted:

$$(7) \qquad [Ca^{2+}]_{SS} = [Ca^{2+}]_0 - (Ca^{2+}{}_{up}/Q)$$

where $[Ca^{2+}]_{SS}$ is the Ca^{2+} concentration in the lake that will exist at steady state under a given harvesting practice, and

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$[Ca^{2+}]_0$ is the pre-industrial Ca^{2+} concentration calculated using eq. 2.

Input data

All available chemical data were gathered for lakes in each of the four regions in south-central Ontario (Fig. 1). These data were collected during the course of a number of different research projects and lake surveys during the period 1981–1995, with most of the data collected between 1983 and 1988. In total, 1337 lakes ranging in size from 0.2 to 12 205.8 ha (median, 27.5 ha; Table 1) had suitable data. All lakes were analysed for alkalinity, conductivity, pH, and major cations and anions (see Table 1 for selected variables). Chemical analyses were carried out at Ontario Ministry of the Environment laboratories; methods are described in detail in Ontario Ministry of the Environment (1983). Further details are given in Henriksen et al. (2002).

Sodium has been excluded from all calculations because of road salt contamination in some of the lakes, although inputs of Na^+ in deposition are low because of the large distance to the nearest ocean. Concentrations of NO_3^- have also been ignored in the current calculations as data are not available for all lakes and, in general, the concentrations are negligible. If NO_3^- were included, the number of lakes that exceed the CL(A) would increase slightly.

In addition to chemical data, the SSWC model requires measured or estimated runoff within each lake's catchment. Runoff coefficients ($m \cdot year^{-1}$) were interpolated from measured 30-year annual average runoff at all long-term hydrologic gauging stations throughout Ontario to produce a provincial runoff map. The 30-year annual average runoff for all lakes is 482 $mm \cdot year^{-1}$ (Table 1).

Estimates of base cation removals resulting from forest harvesting do not exist for the study region. In this study, it is important to note that we are investigating the potential impact of harvesting on lake chemistry by using a range of harvesting estimates and applying the four scenarios to all lakes. The true impact of harvesting can only be assessed once base cation removals for the region (at each site) are known. Furthermore, additional base case losses that may occur immediately following harvest because of altered flow paths or decreased base cation dry deposition, for example, or the release of base cations from the decomposition of organic matter, are not considered in this steady-state model. Net base cation removals due to harvesting (BC_{up}) were estimated using the current base cation pools in 65- to 85-year-old forests measured at seven catchments in south-central Ontario (Watmough and Dillon 2003*b*). These catchments included both hardwood- and softwood-dominated forests (Watmough and Dillon 2003*b*). Current base cation pools in aboveground biomass (Ca, 18.2–31 $kequiv. \cdot ha^{-1}$; Mg, 2.6–4.4 $kequiv. \cdot ha^{-1}$; K, 4.3–6.3 $kequiv. \cdot ha^{-1}$) are within the range reported for mixed hardwood forests in eastern North America (Federer et al. 1989; Adams et al. 2000). Base cation uptake rates were determined based on current base cation pools and forest age assuming (*i*) wood-only (stems without bark) removal, (*ii*) stem-only removal, and (*iii*) whole-tree harvest in an attempt to gauge the potential impact of various harvesting practices in the region. Estimated net base cation removals through the three harvesting types range from 9.9 to 40.8 $mequiv. \cdot m^{-2} \cdot year^{-1}$ (Table 2).

Bulk deposition of SO_4^{2-} has been measured in Muskoka and Haliburton since 1976 (Dillon et al. 1988; Eimers and Dillon 2002). It is assumed that deposition measured at monitoring stations in Muskoka–Haliburton is representative of the entire study region. Exceedance of critical load has been calculated using annual average (1995–1999) bulk SO_4^{2-} deposition (41.1 $mequiv. \cdot m^{-2} \cdot year^{-1}$).

Results and discussion

Exceedance of critical load

If harvesting does not occur, 8.7% of lakes in the study region exceed the CL(A) (Fig. 2). In contrast, assuming wood-only, stem-only, or whole-tree harvesting, the number of lakes that exceed the CL(A) increases to 23.0%, 56.2%, and 71.7%, respectively. These calculations are based on bulk SO_4^{2-} deposition measured between 1995 and 1999. However, SO_4^{2-} export from catchments in the region greatly exceeds input (up to 100%) in bulk deposition (Eimers and Dillon 2002; Watmough and Dillon 2003*b*), and the mean SO_4^{2-} deposition reported for 1995–1999 may also underestimate bulk SO_4^{2-} deposition as 1998 and 1999 were extremely dry years. If SO_4^{2-} export, an estimate of dry deposition input to the surrounding forest, or an increase in SO_4^{2-} bulk deposition were included in the calculation, the number of lakes that exceed the critical load would increase substantially. Likewise, inclusion of NO_3^- in the calculations would also result in an increase in the number of lakes that exceed the critical load, even though NO_3^- concentrations in lakes in the region are low (<2 $\mu equiv. \cdot L^{-1}$ in general). Furthermore, SO_4^{2-} and NO_3^- exports from forested catchments in the region exhibit tremendous year-to-year variation (up to 10-fold), largely resulting from climate variations (Eimers and Dillon 2002; Watmough and Dillon 2003*b*). Large increases in SO_4^{2-} and NO_3^- exports in certain years could lead to exceedance of the critical load, despite the fact that SO_4^{2-} deposition complies with critical load targets. These effects will become more apparent when soils are close to steady state and no longer have the base cation reserves to buffer excess SO_4^{2-} and NO_3^- in soil leachate. Therefore, exceedance values reported here may be viewed as conservative estimates.

The increase in number of lakes that exceed critical load is due to lower base cation inputs to lakes when forests in the surrounding catchments are harvested. Estimates of base cation removals during harvesting used in this study are relatively low. Much higher harvesting removal values have been estimated for similar forest types in eastern North America (Ouimet et al. 2001). Furthermore, Adams (1999) has suggested that base cation removals during selection cutting may be much greater than removals through other common harvesting practices such as clear-cutting. This study was designed to assess the potential impact of harvesting on lake chemistry and may underestimate removals in some areas, whereas there are many areas that experience no harvesting at all. More detailed information on base cation removals through various harvesting practices is urgently needed to calculate the true impact of harvesting on lake chemistry in the region.

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Table 1. Summary statistics for lake area, runoff, and selected chemical variables for lakes (n = 1337) in south-central Ontario.

	Lake area, ha	Runoff, mm	pH	Ca^{2+}, $\mu equiv.\cdot L^{-1}$	Mg^{2+}, $\mu equiv.\cdot L^{-1}$	K^{+}, $\mu equiv.\cdot L^{-1}$	SO_4^{2-}, $\mu equiv.\cdot L^{-1}$
Minimum	0.2	297	4.22	25.2	11.9	2.6	53.2
5 percentile	4.5	413	5.33	90.0	37.5	7.2	101.7
25 percentile	12.7	447	5.94	119.8	51.1	9.7	136.4
50 percentile	27.5	483	6.26	144.7	64.3	11.8	153.4
75 percentile	77.6	515	6.58	174.7	82.4	14.8	170.3
95 percentile	455.0	566	7.09	347.3	140.0	20.9	201.7
Maximum	12 205.8	591	8.10	1986.0	1285.0	45.0	602.1
Mean	128.6	482	6.25	174.3	74.6	12.7	154.1

Table 2. Average values ($mequiv.\cdot m^{-2}\cdot year^{-1}$; (minimum–maximum)) for calcium, magnesium, potassium, and base cation (BC) removals under different harvesting practices.

Harvesting practice	Ca^{2+}	Mg^{2+}	K^{+}	BC
Wood only[†]	5.7 (4.4–6.5)	1.7 (1.3–2.0)	2.5 (2.2–2.8)	9.9 (8.0–11.2)
Stem only	21.4 (17.0–27.5)	2.4 (2.0–2.8)	3.7 (3.3–4.1)	27.5 (22.3–34.3)
Whole-tree	31.0 (24.6–38.8)	3.8 (3.3–4.3)	6.0 (5.4–6.6)	40.8 (33.3–49.7)

[†]Stem without bark.

Fig. 2. Impact of different harvesting practices on the number of lakes with exceedance of critical load: (*a*) no harvesting, 116 lakes (8.7%); (*b*) wood-only (stem without bark) harvesting, 308 lakes (23.0%); (*c*) stem-only harvesting, 752 lakes (56.2%); and (*d*) whole-tree harvesting, 958 lakes (71.7%). See Fig. 1 for map projection.

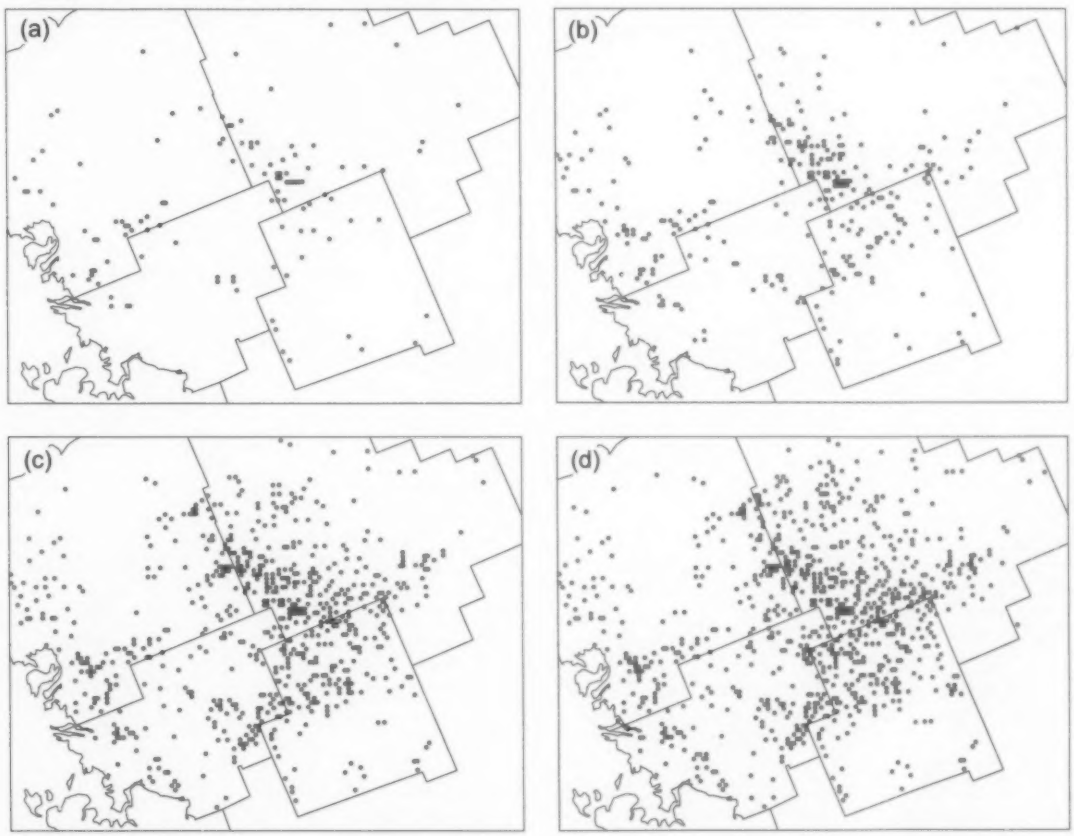

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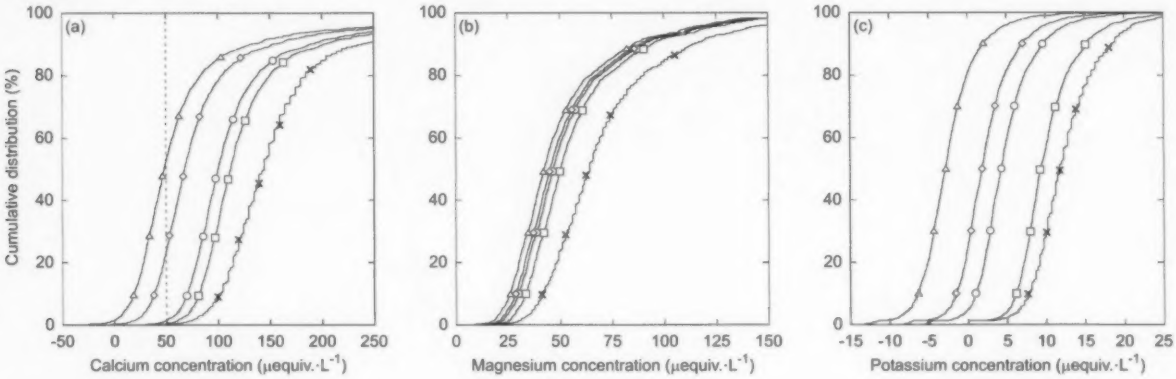
Fig. 3. Cumulative distribution function of the impact of harvesting practices on (*a*) calcium lake concentrations (threshold concentration of 50 μequiv.·L^{-1} shown as dotted line); (*b*) magnesium lake concentrations; and (*c*) potassium lake concentrations. ×, current concentrations; □, steady-state concentrations; ○, wood-only harvesting (stem without bark); ◇, stem-only harvesting; triangle, whole-tree harvesting).

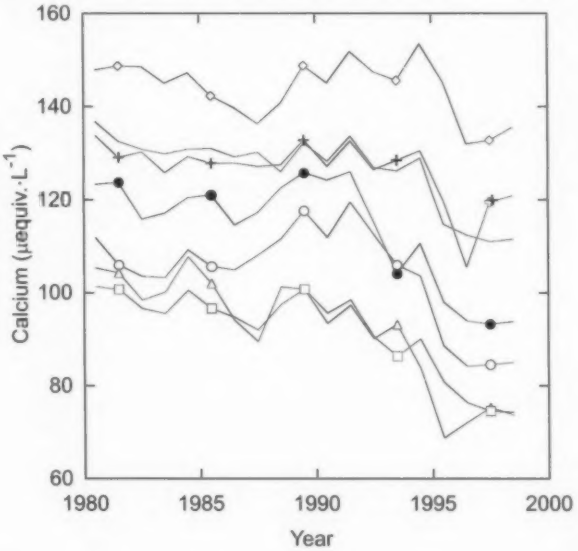


Base cation concentrations in lakes

Our calculations suggest that base cation concentrations in lakes will decrease dramatically under the various harvesting scenarios (Figs. 3 and 4). However, in some areas, particularly those characterised by extremely shallow soils (<0.5 m), it is questionable whether the highest level of harvesting would be sustainable because of the extremely low base cation leaching losses that are predicted at critical load. For example, it was calculated that Ca^{2+} concentrations in soil leachate below the rooting zone would reach a steady-state concentration of 9–27 μequiv.·L^{-1} if stem-only harvesting continues at catchments in Muskoka and Haliburton (Watmough and Dillon 2003*a*). These concentrations are 70–80% lower than current leaching losses. Clearly, research is required to determine whether low leaching losses that are predicted at steady state under some harvesting scenarios are sustainable with respect to forest health, productivity, and diversity. If rates of forest growth decrease as a result of declining soil exchangeable base cation pools, then net annual base cation uptake rates will be lower and base cation leaching losses from soil (and therefore inputs to lakes) will be higher than predicted.

If we assume that all of the forest harvesting scenarios considered in this study are sustainable, then Ca^{2+} concentrations in lakes will decrease dramatically (Fig. 3*a*). Decreases in lake Ca^{2+} concentration have already occurred in the region (Fig. 4), and similar decreases in lake Ca^{2+} have been reported in other parts of Ontario (Keller et al. 2001), eastern Canada (Clair et al. 2002), and the northeastern United States (Driscoll et al. 1995). Low Ca^{2+} levels in lakes may have serious biological implications (Malley 1980; St. Louis and Barlow 1993), and an $[ANC]_{limit}$ of 40 μequiv.·L^{-1} may be less meaningful at extremely low lake Ca^{2+} concentrations (Hessen et al. 1995). For example, recent reports have suggested that a decrease in lake Ca^{2+} may increase the sensitivity of aquatic biota to ultraviolet (UV) radiation (Hessen and Rukke 2000). Some workers have suggested that a critical Ca^{2+} threshold for lakes lies between 25 and 50 μequiv.·L^{-1} (Hessen et al. 2000). Using a critical Ca^{2+} threshold of 50 μequiv.·L^{-1} as an example, in this study only four of the 1337 lakes surveyed (0.3%) will have Ca^{2+} concentrations below the critical value

Fig. 4. Changes in calcium concentrations in eight intensively studied lakes in south-central Ontario. ◇, Harp Lake; line, Red Chalk Lake; +, Blue Chalk Lake; ●, Chub Lake; ○, Crosson Lake; △, Heney Lake; □, Plastic Lake.



if harvesting does not occur (Fig. 5). If only wood is removed, 19 lakes (1.4%) will have Ca^{2+} concentrations below 50 μequiv.·L^{-1}, and if stem-only harvesting occurs, this number increases to 311 (23.3%). Finally, if whole-tree harvesting occurs, 695 (52%) lakes will ultimately have Ca^{2+} concentrations below 50 μequiv.·L^{-1}.

The implications for lake Mg^{2+} concentrations are much less dramatic (Fig. 3*b*), because harvest removals of Mg^{2+} are low relative to weathering rates in the region. In contrast, the impacts of harvesting on lake K^+ levels are enormous, particularly under conditions that assume whole-tree harvesting (Fig. 3*c*). These calculations indicate that lake K^+ concentrations would be less than 0 μequiv.·L^{-1} (i.e., harvesting is not sustainable) in about 80% of the lakes if whole-

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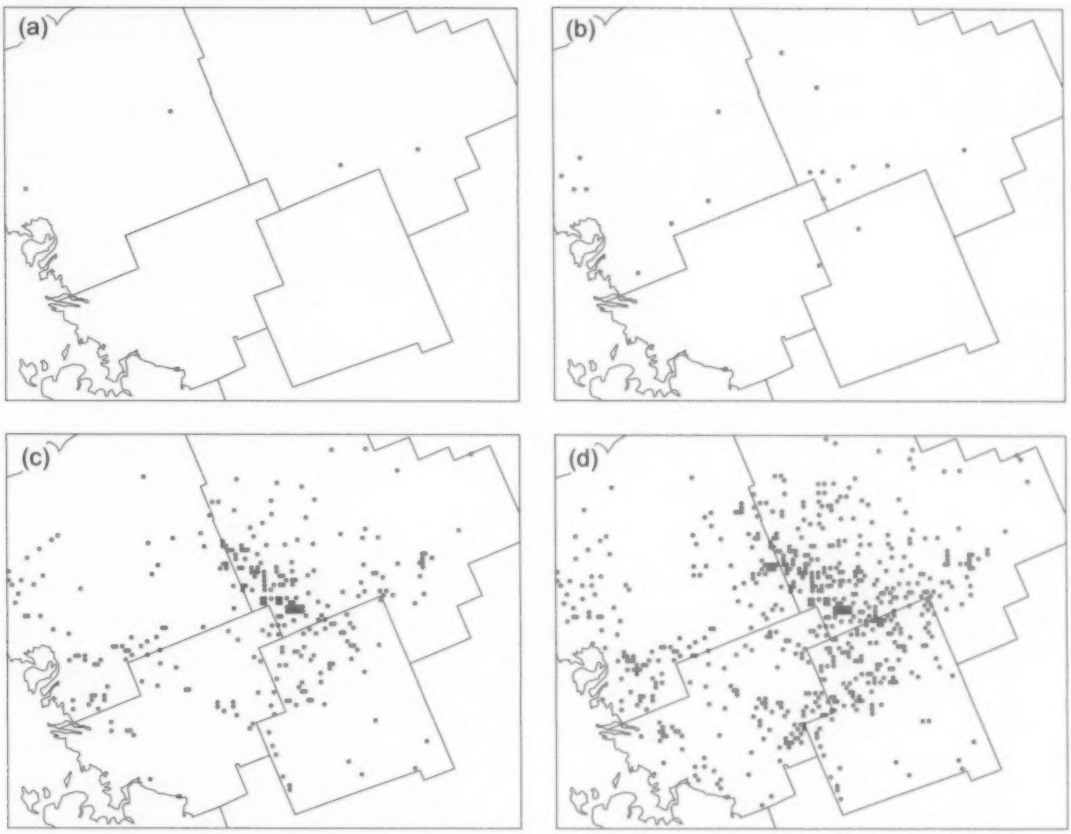
Fig. 5. Impact of harvesting on calcium lake concentrations. Maps depict the number of lakes that exceed the calcium threshold concentration (50 μequiv·L^{-1}) under different harvesting practices: (*a*) no harvesting, four lakes (0.3%); (*b*) wood-only (stem without bark) harvesting, 19 lakes (1.4%); (*c*) stem-only harvesting, 311 lakes (23.3%); and (*d*) whole-tree harvesting, 695 lakes (52.0%). See Fig. 1 for map projection.



tree harvesting occurs. However, calculations in this study are very likely to overestimate the impact of harvesting on lake K^+ levels because K^+ is treated in the same way as Ca^{2+} and Mg^{2+} when calculating the lake concentrations at steady state. Base cation concentrations in lakes under the various harvesting scenarios were calculated using the same *F* factor for each base cation (see eq. 2). This calculation assumes that current losses of Ca^{2+}, Mg^{2+}, and K^+ from the exchangeable pool are all occurring at the same rate, which is determined by the *F* factor. However, mass balance calculations for terrestrial catchments in the region indicate that only Ca^{2+} and Mg^{2+} are currently being lost from the exchangeable pool to any great extent; K^+ appears to be in balance (Watmough and Dillon 2003*b*). As a result, the approach used in this study will likely underestimate the impact of harvesting on lake Mg^{2+} and Ca^{2+} concentrations because losses of these base cations will be slightly greater (make up a larger proportion of the current base cation leaching). In contrast, the impact of harvesting on lake K^+ levels will be overestimated as our calculations assume that K^+ is being lost from the exchangeable soil pool at the same rate as Ca^{2+} and Mg^{2+}. Nevertheless, K^+ levels in lakes in the region are low, and harvesting may be expected to substantially reduce lake K^+ levels, particularly given the relative efficiency by which trees can retain K^+ (Johnson et al. 1985). The impacts of such low K^+ levels on lake biota are currently unknown.

These predictions are based on a steady-state model; however, dynamic models offer an opportunity to determine the level of deposition reduction required to achieve a given water chemistry target within a specified time scale (Cosby et al. 2001). Furthermore, the impact of land-use changes such as harvesting on water chemistry, in combination with changes in acid deposition, can only be determined using dynamic modelling approaches. However, current exchangeable base cation pools in the region are low, and in many cases, the base cation pool held in biomass exceeds that in soil (Watmough and Dillon 2003*b*). This indicates that at current deposition values and assumed harvesting rates, dramatic changes in lake base cation concentration and ANC may be expected within only a few decades. In summary, forest harvesting in south-central Ontario will potentially have a dramatic impact on lake chemistry, yet harvest removals on a spatial scale are currently unknown. Any harvesting will ultimately lead to lower base cation concentrations in lakes as exchangeable base cation pools in soil decline. Calculations in this study suggest that harvesting will lead to

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dramatic reductions in lake base cation levels and that many lakes will exceed the CL(A) unless substantial decreases in SO_4^{2-} deposition occur. In particular, Ca^{2+} concentrations in lakes are predicted to decline rapidly in regions that are harvested with potentially damaging effects on biota. As soils approach steady state (i.e., are no longer acidifying), the ability of soils to buffer against acid leaching will decrease and climate-induced increases in SO_4^{2-} and NO_3^- export may have even more serious biological implications. Ultimately, the base cation inputs to lakes will be determined by the rate of mineral weathering, base cation deposition, and the level of harvesting. One key area of future research will be to evaluate the consequence of these low base cation concentrations in lakes.

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Bimodal size distributions in Arctic char, *Salvelinus alpinus*: artefacts of biased sampling

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Abstract: Bimodal population size and age distributions in Arctic char (*Salvelinus alpinus* (L.)) and hypotheses on growth patterns generating bimodality have drawn considerable attention during the last decade. However, such bimodality has also been suggested to be an artefact of biased sampling. We examined published data sets reporting bimodal size distributions in gill-net samples of Arctic char in order to confront hypotheses on growth patterns generating bimodal population size distributions. Growth patterns were derived from published length-at-age data. Simulations revealed that the observed growth patterns evidently could not generate a bimodal population size distribution. The basic reason for this was that growth did not stagnate strongly enough in the largest size classes of Arctic char. The reliability of growth approximations from length-at-age data was supported by empirical data on back-calculated growth trajectories. Furthermore, differences in year-class strength cannot explain all of the observed bimodal size and age distributions in gill-net samples, as they have been reported to persist over time. Thus, bias in the sampling procedure, which overestimates the frequency of old and large fish, is retained as the only plausible explanation for stable bimodal size distributions often observed in Arctic char gill-net samples.

Résumé : Depuis une dizaine d'années, on s'intéresse beaucoup aux distributions bimodales des tailles et des âges des populations d'ombles chevaliers (*Salvelinus alpinus* (L.)), ainsi qu'aux hypothèses qui tentent, à partir des patterns de croissance, d'expliquer cette bimodalité. Certains croient, cependant, que la bimodalité peut être un artefact dû à un échantillonnage faussé. Nous avons examiné des séries de données tirées de la littérature qui présentent des distributions bimodales des tailles dans des captures d'ombles chevaliers au filet maillant pour comparer les hypothèses explicatives des distributions bimodales. Des données de longueurs aux différents âges ont servi à établir les patterns de croissance. Des simulations révèlent que les patterns de croissance observés ne peuvent, de toute évidence, générer une distribution bimodale des tailles dans les populations; la raison principale en est que la croissance ne stagne pas suffisamment dans les classes de tailles les plus fortes de l'omble chevalier. La fiabilité des approximations de croissance obtenues à partir des données de longueurs aux différents âges est confirmée par des données empiriques sur des trajectoires de croissances obtenues par rétro-calcul. De plus, les différences de force des classes d'âge ne peuvent expliquer toutes les distributions bimodales de tailles et d'âges observées dans les récoltes au filet maillant, car, d'après la littérature, celles-ci se maintiennent dans le temps. Nous retenons donc les erreurs dans les méthodes d'échantillonnage qui semblent surestimer les fréquences des poissons de grande taille et des poissons âgés comme la seule explication plausible des distributions bimodales stables des tailles qui sont fréquentes dans les échantillons d'ombles chevaliers récoltés au filet maillant.

[Traduit par la Rédaction]

Introduction

Size distributions with two distinct size modes (bimodal size distributions) have been observed in a variety of species of plants and animals. Two different general types of bimodality have been discussed in the ecological literature: (1) population bimodality, observed in the size distribution that includes all age classes of the population, and (2) cohort bimodality, observed within a single developing cohort. The findings of population bimodality in Arctic char (*Salvelinus alpinus* (L.)) have recently been treated in a number of papers (e.g., Griffiths 1994; Vanriel and Johnson 1995; Hammar 2000). Qualitative explanations for the formation of bimodality have been proposed, ranging from complex ontogenetic growth and mortality patterns (e.g., Johnson 1976; Vanriel and Johnson 1995) to cannibalism and parasitism (Svenning and Borgstrøm 1995; Reist et al. 1995; Hammar 2000).

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A population's size distribution is formed by its recent history of recruitment and mortality, integrated with individual growth (e.g., Power 1978; Botsford et al. 1994, Claessen and de Roos 2003). Griffiths (1994, fig. 1) identified four different ways in which a bimodal population size distribution of Arctic char could be formed (hereafter referred to as types *i*, *ii*, *iii*, and *iv*). Type *i* bimodality arises from differences in year-class strength, i.e., strong cohorts (abundant numbers) form distinct size modes as they grow. Formation of type *i* bimodality is based on a nonstable population age structure. Types *ii–iv* may generate bimodal size distributions under the assumption of stable age structures. In all three instances (types *ii–iv*), the first size mode would consist of abundant young and small fish. Essential for the formation of a second size mode of larger fish in types *ii–iv* is a stagnation in growth for individual fish as they approach an asymptotic large size for the population. Furthermore, large fish must survive to allow for an accumulation of slowly growing individuals approaching this asymptotic size. The differences between Griffith's (1994) types *ii*, *iii*, and *iv* rely on individual growth patterns. In type *ii*, individual growth rates simply decrease as size increases. The third scenario (type *iii*) is similar to that of the "double growth curve" (see Claessen et al. 2000) in which there is a stagnation in growth at some small size, followed by an abrupt increase in growth and a final growth stagnation at some larger size. The fourth scenario (type *iv*) involves a cohort split in slow-growing and fast-growing individuals.

Apart from biological explanations, there may be a methodological explanation for the occurrence of bimodal population samples of Arctic char. Population samples are usually obtained with gill nets consisting of a series of different mesh sizes, with the aim to sample a representative size distribution of the population. However, even the most advanced gill-net series may show size-dependent selectivity and therefore produce biased estimates of the true population size structure (e.g., Jensen and Hesthagen 1996; Finstad et al. 2000). Nevertheless, robustness of gill nets as a method for assessing population size and age structures has been argued for (e.g., Hammar 2000).

Here, we aim at testing the predictions by Griffiths (1994) regarding possible growth patterns generating observed bimodal size distributions in Arctic char population samples (i.e., types *ii*, *iii*, and *iv*). Our hypothesis is that the observed growth patterns may not enable the formation of bimodal population size distributions inferred from gill-net samples. A key feature of the growth patterns in this respect is stagnation in growth at some size, enabling the formation of a second size mode.

Bimodal size and age distributions in gill-net samples have previously been reported to persist over long periods of time in some Arctic char populations (e.g., Johnson 1983; Svenning and Borgstrøm 1995). This indicates that the observed bimodality can be generated without assumptions of year-class fluctuations, on which the type *i* explanation is based. Therefore, in the present study, we only consider the scenarios of types *ii–iv* for generating bimodality. We surveyed a number of published reports on bimodal population size distributions in Arctic char that were presented with length-at-age figures. These data sets were used to derive individual growth patterns. As reliable estimates of mortality were not accessible, we varied the age-specific mortality rates and tested if the observed growth patterns could generate bimodal population size distributions. This approach presupposes that empirical growth patterns obtained from length-at-age data reflect the true growth pattern of individual fish. This assumption was supported by empirical data on back-calculated individual growth trajectories from a Norwegian alpine population of Arctic char displaying a bimodal population size distribution in multimesh gill-net samples.

Materials and methods

Back-calculation of growth trajectories

Fish were sampled in Store Skarddørsjø (62°51′N, 12°05′E), Central Norway, which is an ultraoligotrophic monomictic alpine lake (1058 m above sea level (asl)). The lake holds a stationary allopatric population of Arctic char, and cannibalism is frequent in the largest size classes. Fish were sampled with bottom multimesh gill nets of the NORDIC series (Appelberg et al. 1995) (1.5 m × 30 m; bar mesh size 5–55 mm) in August 2001. The gill nets were set perpendicular from the shore down to a maximum depth of 20 m. The nets were set in the evening and hauled next morning after ca. 12 h. Previous studies of similar neighbouring systems (Schartau et al. 1994), as well as echo-sounder surveys during the present sampling, did not reveal pelagic behaviour of the char. Floating gill nets were therefore not used.

Total fish length was measured to the nearest millimetre with the tail spread in a natural position, and the fish were aged using sacculus otoliths. Otoliths were also used for back-calculation of growth. Measures of otolith radii and distances to each annulus were obtained with a stereoscopic dissecting microscope. Otoliths that were broken or had a doubtful annulus structure were excluded from further analyses. The relationship between otolith size and total length and age was estimated using linear regression on natural log transformed values of otolith size and length. This resulted in regressions with normally distributed variance and no indication of size trends in residual deviations from predicted values. Individual length at previous ages was calculated according to a modification of the Morita and Matsuishi (2001) method, including the interaction term (Finstad 2003).

Simulating population size distribution based on observed growth patterns

To test whether growth patterns for Arctic char were consistent with bimodal population size structures, population size distribution was simulated as a function of empirical growth patterns and variable mortality. For simplicity, stable age distributions were assumed (see Introduction). We classified populations a priori to Griffith's (1994) type *iii* or type *iv* growth patterns by visually inspecting length-at-age plots. In the data sets examined, a typical type *ii* growth pattern did not appear and this scenario was therefore omitted from further analyses. In an initial cohort (N = 10 000), individual fish were assigned to a growth pattern in which length-at-age was given by either a sigmoid or a von Bertalanffy growth function (eqs. 1 or 2 below), and parameter values were drawn at random from a normal distribution. Because of problems in interpreting the number of fish in the samples (it is not possible to infer from length-at-age plots if points

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represent one or several individuals), estimates of growth parameter variances are confounded with uncertainties. Therefore, in subsequent analyses, variance in the growth parameters was varied to investigate its potential influence on the population size distribution.

The mortality rate was defined as the probability of dying during a time period of 1 year. Mortality rate as a function of age (eq. 3) was modelled by drawing the individuals to go out of the model (i.e., dying) at random when growing from one age group to the next. This event was drawn from a binominal distribution with the probability of a given outcome depending on age and given by eq. 3.

For populations exhibiting a type *iv* growth pattern, an "upper-mode" or a "lower-mode" growth pattern was assigned at random to individuals in the initial cohort. The proportions of upper-mode or lower-mode individuals were varied in the subsequent analyses. The different groups were also assigned to different mortality regimes by varying the parameters of the mortality function.

We derived growth patterns for Arctic char by using data from published length-at-age plots. The figures were scanned and Cartesian co-ordinates of individual fish were read using the software ImageJ (http://rsb.info.nih.gov/ij). The age and length of individual fish were then assessed by scaling of the co-ordinates according to length and age measures in the figure.

In populations assumed to generate bimodality by a type *iii* growth pattern, growth was modelled as a sigmoidal function of age:

$$(1) \qquad L(a) = X/(1 + \exp(-((a - Z)/Y)))$$

where $L(a)$ is the length measurement (mm) at age a (years), and X, Z, and Y are constants estimated by the Marquardt–Levenberg algorithm (Press et al. 1986) using Sigmaplot 2001.

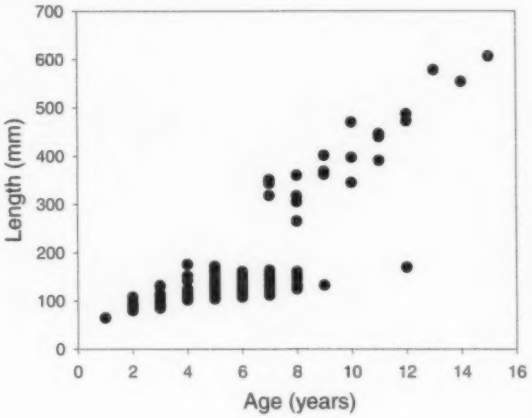
To estimate the different growth patterns in populations displaying within-cohort differences in growth (type growth pattern), we differentiated the data into two groups following the approach in Griffiths (1994). All fish younger than the age at which the within-cohort split in growth appears (LENSPLIT; fig. 2 in Griffiths 1994) were included in estimating both the upper- and lower-mode growth curves. The von Bertalanffy growth function was then fitted to the separate groups:

$$(2) \qquad L(a) = L_\infty(1 - \exp(-k(a - t_0)))$$

where $L(a)$ is the length measurement (mm) at age a (years), and t_0, k, and L_∞ are constants estimated similar to those in eq. 1.

To test the accuracy of our approach (i.e., deriving growth function parameters using co-ordinates from published length-at-age plots), the data from Store Skarddørsjø were plotted (Fig. 1) and the length-at-age of individual fish was determined by using the Cartesian co-ordinates following the same method as that used for the published data sets. This procedure was repeated 15 times, and the parameters of the growth function were estimated for each of the 15 generated data sets. The estimated parameters mean L_∞ = 193 476 (± 4781 standard error, SE), mean t_0 = 0.81 (± 0.20 SE), and mean k = 0.0002 (± 1.5 × 10^{-5}) for the upper mode and

Fig. 1. Length-at-age plot for Arctic char (*Salvelinus alpinus* L.) sampled with NORDIC multimesh gill nets in Store Skarddørsjø (N = 211).



mean L_∞ = 144 (± 2.2 SE), mean t_0 = –0.08 (± 0.20 SE), and mean k = 0.53 (± 0.07) for the lower mode were all within 95% confidence limits of the parameter estimates from the original data. Sensitivity analyses of the model (see Results and Discussion sections) indicated that the error in the parameter estimation resulting from our approach using published figures is far too small to alter any of our conclusions.

A prerequisite for generating a bimodal size distribution is a decrease in the specific mortality rate with increasing age (e.g., Power 1978; Botsford et al. 1994). We modelled the probability of surviving (s) to a given age class as an inverse exponential function of age, yielding an asymptotic decrease in mortality with increasing age

$$(3) \qquad s = (c + d)/(d + \text{age})$$

where "age" is the age in years and c and d are positive parameters. Because it was not possible to estimate mortality from available data, we varied the parameters of eq. 3 to investigate the effect on the resulting population size distribution. Maximum age was set to 25 years for simulated populations following a type *iii* growth pattern and 20 years for simulated populations following a type *iv* growth pattern, which agrees with the published literature (references in Tables 1 and 2).

Results

Back-calculation of growth trajectories

The NORDIC mulitmesh gill-net catches from Store Skarddørsjø consisted of Arctic char with total length ranging from 66 to 606 mm and age ranging from 2 to 15 years. The length-at-age plots are characterised by a notable lack of fish in intermediate size classes as very few individuals of sizes 170–250 mm were sampled. The size distribution in the gill-net sample of the population was therefore bimodal, with the lower mode containing fish in the size range 70–180 mm, and the upper mode, 250–600 mm (Fig. 1). The length-at-age of Arctic char in Store Skardørsjø indicated two different growth strategies within the population. Although some fish stagnate in growth at the age of 4–5 years and at a size of 100–150 mm, part of the population continued to grow throughout

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Table 1. Estimated constants (X, Z, and Y) for the sigmoidal growth function (eq. 1) assigned to Arctic char populations displaying a type *iii* growth pattern.

Lake	X	Z	Y	Reference
Johansvatn[a]	558.68	4.001	12.58	Hammar (2000)
Wibjørnvatn	493.02	4.12	10.34	
Annavatn	457.79	2.96	12.17	
Arresjøen[a]	554.82	5.96	15.18	Svenning and Borgstrøm (1995)

Note: The parameters were estimated from published length-at-age plots. All the populations are located on the islands of Spitsbergen.

[a]Johansvatn and Arresjøen refer to the same lake, which is named differently by different authors (Martin Svenning, Norwegian Institute of Nature Research, N-9296 Tromsø, Norway, personal communication). Samples presented in Hammar (2000) were obtained in 1981, whereas samples presented by Svenning and Borgstrøm (1995) were obtained in 1990, 1993, and 1994.

Table 2. Estimated constants (L_∞, k, t_0) for the von Bertalanffy growth function (eq. 2) for upper- and lower-mode Arctic char populations displaying a cohort split (type *iv*) growth pattern.

		Upper mode			Lower mode			
Location	Lake	L_∞	k	t_0	L_∞	k	t_0	Reference
Bear Island	Stevatn	28 259	0.01	–0.48	155	0.14	–135	Klementsen et al. (1985)
	Ellasjø	811	0.04	0.56	538	0.001	–231	
Canada	Small but Windy Lake	10 489	0.0032	–1.14	187	0.38	–0.58	Hammar (1998)
Scandinavia	Store Skarddørsjø	155 660	0.0002	1.12	160	0.26	–0.98	Present study

Note: The parameters were estimated from published length-at-age plots.

Fig. 2. The mean back-calculated growth (± standard deviation) for cohorts 1990 to 1997 of upper-mode (open symbols) and lower-mode (solid symbols) Arctic char (*Salvelinus alpinus* L.). The definition of group assignment of the individuals is given in Material and methods.

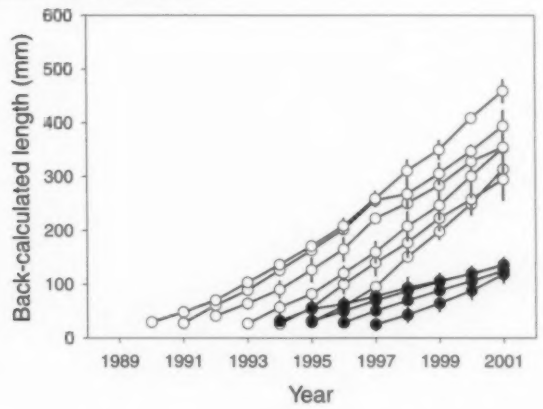
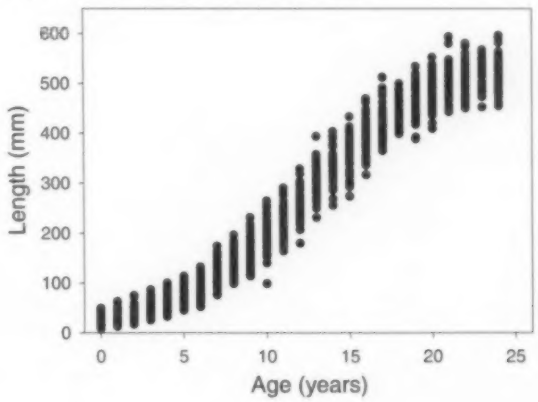


Fig. 3. Simulation of the length-at-age pattern for the sigmoidal growth model parameterised with empirical data from the Arctic char (*Salvelinus alpinus* L.) population in Johansvatn (Hammar 2000). Parameter values are given in Table 1.



the recorded life span. This within-cohort split in growth took place at an age of about 4–5 years. Back-calculation of growth in age-4+ or older Arctic char was fairly linear with time (Fig. 2). It was also apparent that consecutive cohorts displayed similar growth patterns in both upper- and lower-mode Arctic char, respectively (Fig. 2).

Simulating population size distributions based on observed growth patterns

We found eight Arctic char populations that were reported to show bimodal size distributions and for which length-at-age figures have been presented. Based on the length-at-age figures, we assigned a type *iii* growth pattern to four of these populations (Table 1) and a type *iv* growth pattern to four populations (Table 2). As a baseline for testing if a type *iii* growth pattern could generate a bimodal population size distribution, we parameterised the sigmoidal growth function with empirical data from Johansvatn, Spitsbergen (Table 1; Fig. 3). The resulting growth pattern did not support a pronounced stagnation in growth in large char (Fig. 3). Combining the resulting growth pattern with a mortality rate set to decrease from 0.45 in the youngest age class (1 year) to 0.04 in the oldest age class (25 years) did not generate a bimodal size distribution (Fig. 4*a*). A prolonged right-hand tail of large fish in the population, however, was apparent (Fig. 4*b*). To obtain a distinct bimodal size distribution, a pronounced decrease in mortality had to be imposed on the

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Fig. 4. Distributions of (*a*, *c*) age and (*b*, *d*) length from the simulated sigmoidal growth pattern illustrated in Fig. 3. The mortality rate (solid line) was set to gradually decrease from 0.45 to 0.04 (*a* and *b*) and from 0.12 to 0.04 (*c* and *d*) with increasing age.

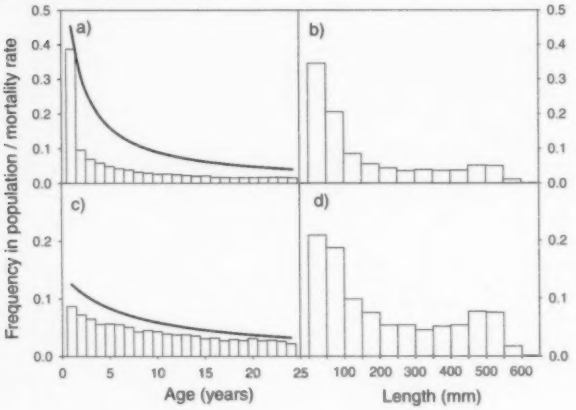
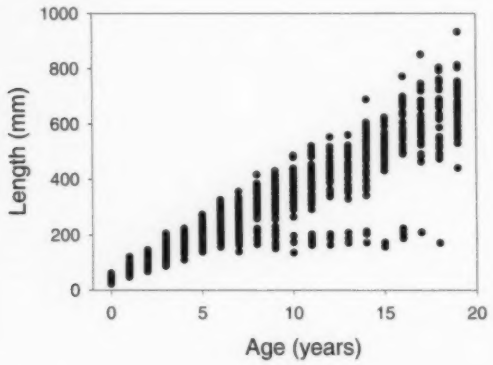


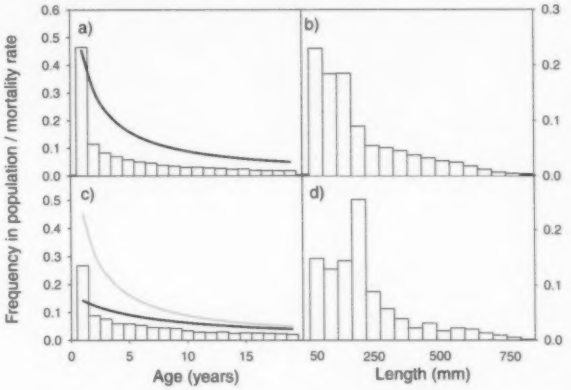
Fig. 5. Simulated length-at-age pattern for a type *iv* growth pattern parameterised with empirical data from Small but Windy Lake (Hammar 1998). Parameter values for the growth functions of upper- and lower-mode Arctic char (*Salvelinus alpinus* L.) are given in Table 2.



population. In Figs. 4*c* and 4*d*, mortality rate was set to decrease from 0.12 in the youngest age class (1 year) to 0.03 the oldest age class (25 years). Such a low rate of mortality implied that nearly 30% of the individuals survived from the age of 1–25 years (Fig. 4*c*). Varying the standard deviation (SD) of the growth parameters in the range from 5% to 25% of the mean value did not influence the basic properties of the population size distribution. Growth patterns from Arctic char populations originating from Annavatn, Wibjørnvatn, and Arresjøen were examined similarly to those of populations from Johansvatn, with mortality rates as in Fig. 4*a*. A pronounced stagnation in growth did not appear in any of these populations, and none of the estimated parameter values gave rise to bimodal population size distributions (Table 1).

The model with a type *iv* growth pattern was first parameterised with estimated growth curves from the Small but

Fig. 6. Distributions of (*a*, *c*) age and (*b*, *d*) length from the cohort split in growth pattern illustrated in Fig. 5. The mortality rate (solid line) was set to gradually decrease from 0.45 to 0.05 for both lower- and upper-mode growth patterns (*a* and *b*). In panels (*c*) and (*d*), the mortality rate (grey line) was reduced to gradually decrease from 0.14 to 0.05 for the lower-mode growth pattern. The mortality rate for upper-mode growth was not changed compared with (*a*) and (*b*).



Windy Lake (Table 2). No stagnation in growth appeared in the upper-mode char. In contrast, the lower-mode char stagnated in growth at a size close to 150 mm (Fig. 5). Combining the resulting growth pattern with a mortality rate set to decrease from 0.45 in the youngest age class (1 year) to 0.05 in the oldest age class (20 years) (Fig. 6*a*) did not generate a bimodal size distribution (Fig. 6*b*). Neither did varying the proportion of individuals assigned with an upper- or lower-mode growth. Increasing the survival of upper-mode individuals or decreasing the survival of lower-mode individuals only prolonged the right-hand tail of the size distribution and did not result in modal formation. However, a second mode did appear at the asymptotic size of lower-mode char when the mortality rate was low enough to allow for an accumulation of slowly growing cohorts (Figs. 6*c*, 6*d*). All of the estimated population growth parameters from populations displaying a type *iv* growth pattern were examined similarly to the Small but Windy Lake data, with mortality rates as in Fig. 6*a* (Table 2). None of the estimated growth parameters generated bimodal size distributions. In contrast, a bimodal population size distribution resulting from an accumulation of upper-mode char was only possible to obtain by a substantial change in the growth function parameters. When using the same mortality regime as in Fig. 6*a*, parameter values of k and L_∞ would have to be set to 0.2 and 600 mm, respectively. This would imply that upper-mode fish would have to reach a mean length of 400 mm in 4 years.

Discussion

Under the assumption of a stable age distribution, it is essential for the formation of a distinct size mode that individual fish stagnate in growth as they approach a given size. Furthermore, survival of slowly growing individuals approaching such a size must be large enough to allow for an accumulation of fish within a distinct size range. Our results

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demonstrated that none of the observed growth patterns gave rise to bimodal size distributions as observed in gill-net samples. This was mainly due to continuous growth in large fish. The back-calculated growth trajectories from large Arctic char were fairly linear with time, and none of the surveyed populations proved to substantially stagnate in growth with increasing size of the fish. A distinct size mode of large fish therefore did not appear in the size distributions generated by the present models, within reasonable mortality regimes of the fish. When using the same mortality regime as in Fig. 6*a*, parameter values of k and L_∞ would have to be set to 0.2 and 600 mm, respectively, to achieve a distinct bimodal size configuration with a second mode consisting of large char. These parameter values imply that upper-mode fish would have to reach a mean length of 400 mm in 4 years.

Pronounced stagnation in growth was observed in lower-mode char from populations classified to a type *iv* growth pattern. Given assumptions of low mortality, this growth pattern was demonstrated to result in a second size mode consisting of lower-mode char. However, this size mode is very different from the second size mode observed in the empirical data occurring at considerably larger sizes.

There is no a priori reason to rule out varying year-class strength as an explanation for bimodal size distributions in Arctic char populations. Nevertheless, the fact that bimodal size and age distributions have been reported to be sustained over long periods of time in some populations (e.g., Johnson 1983; Svenning and Borgstrøm 1995) demonstrates that varying year-class strength is not essential for obtaining bimodal size distributions in Arctic char gill-net samples. A true population, however, obviously cannot attain a bimodal age distribution without nonstable population age structure. A sustained bimodal age distribution, as reported by Johnson (1983) and Svenning and Borgstrøm (1995), strongly suggests that the age distribution in the samples does not reflect the true age distribution in the focal population.

Complex growth patterns are frequently associated with observed bimodal size distributions in Arctic char (e.g., Johnson 1976; Parker and Johnson 1991; Hammar 2000). To explain the observations of bimodality in population samples from Northern populations of Arctic char, lake whitefish (*Coregonus clupeaformis* (L.)), and lake trout (*Salvelinus namaycush* (Walbaum)), Johnson (1976, 1983) initially proposed the hypothesis stating that the main parts of lake habitats are occupied by the upper-modal groups. Recruitment into this mode only occurs after displacement of fish from the main habitat. Recruitment into the main habitat was suggested to result in a rapid increase in growth and a quick approach to the second modal size resulting in the observed bimodal size distribution. However, no complex growth pattern was apparent in the back-calculated growth trajectories from the Store Skarddørsjø samples. It was also apparent from the back-calculated growth patterns that the empirical length-at-age data gave a good approximation to the individual growth trajectories.

Evidently, given stable age structures, none of the biological mechanisms suggested to produce and sustain bimodal size distributions in Arctic char populations is in fact likely to do so. We therefore suggest that the only plausible explanation for the observations of bimodal size and age distributions in gill-net catches of Arctic char is bias in the sampling procedure. Sampling with sets of multimesh survey gill nets is an indirect method to estimate population size structure and is commonly applied in population and monitoring studies of fish (e.g., Jensen 1990; Appelberg et al. 1995). The problem with the multimesh gill-net sampling procedure is that it implicitly assumes equal relative catching efficiencies for all mesh sizes, although they often are unequal (Jensen and Hesthagen 1996). Recently, direct estimates of gill-net selectivity based on known population size distributions (obtained by mark–recapture experiments and by successive removal methods) have demonstrated that relative catching efficiency increases exponentially with increasing mesh size for both brown trout (*Salmo trutta*; Jensen and Hesthagen 1996) and Arctic char (Finstad et al. 2000). As a result, gill-net samples give a biased size and age distribution in which large and old fish will be overrepresented. Reasons for an increase in the relative selectivity of gill nets with increasing mesh size are manyfold and are discussed in length by Finstad et al. (2000).

As a consequence, given a continuous increase in relative catching efficiency with increasing mesh size, a multimesh gill-net sample from a fish population with an exponentially decreasing size structure will show an unimodal size distribution (Finstad et al. 2000). A bimodal sample distribution is achieved if an abrupt increase in the relative selectivity for large-sized fishes is added (Finstad et al. 2000). Finstad et al. (2000) reported the proportion of large char in the multimesh gill-net catches to be 20 times higher than their directly estimated proportion in the focal population. Thus, the higher relative catching efficiency for large char could explain the observed bimodal size distributions with a preponderance of old and large char in the gill-net samples. The high selectivity for large cannibals observed in the catches by Finstad et al. (2000) compared with their proportion in the population could partly be due to the fact that swimming speed and distance travelled tend to increase with fish body size (Blake 1983; Godin 1997). Aside from the effect of increased body size, abrupt size-dependent differences in gill-net capture probability could be due to any factor resulting in a sudden increase in activity of the fish below or above a certain size, such as habitat or diet shifts or predator risk (e.g., L'Abée-Lund et al. 1993; Damsgård and Ugedal 1997).

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Small-scale temporal and spatial variation in Atlantic cod (*Gadus morhua*) life history

Tara M. McIntyre and Jeffrey A. Hutchings

Abstract: Life histories of Atlantic cod (*Gadus morhua*) from the Gulf of St. Lawrence south to Georges Bank differ significantly through time and space. Within the Southern Gulf, fecundity per unit body mass differed by more than 40% over short (2 years) and long (42–45 years) periods of time. Significant variation in size-specific fecundity is also evident among populations: Southern Gulf cod produce almost 30% more eggs per unit body mass than those on Georges Bank, whereas fecundity of Scotian Shelf cod is almost half that of cod in Sydney Bight. Compared with those on Georges Bank, Southern Gulf cod life histories are characterized by high fecundity, late maturity, high gonadosomatic index, and large eggs. Relative to the influence of body size, neither temporal nor spatial differences in fecundity can be attributed to physiological condition, as reflected by liver weight, hepatosomatic index, and Fulton's *K*. Delayed maturity and higher reproductive allotment among Southern Gulf cod can be explained as selection responses to slower growth, higher prereproductive mortality, and fewer lifetime reproductive events. Patterns of covariation in heritable, fitness-related traits suggest the existence of adaptive variation and evolutionarily significant units at spatial scales considerably smaller than the species range in the Northwest Atlantic.

Résumé : Les cycles biologiques des morues franches (*Gadus morhua*) de l'Atlantique, depuis le golfe du Saint-Laurent jusqu'au banc Georges, diffèrent significativement dans le temps et dans l'espace. Dans la partie sud du golfe, la fécondité par unité de masse corporelle varie de plus de 40 % sur des périodes courtes (2 ans) et longues (42–45 ans). Des variations significatives de la fécondité reliée à la taille s'observent aussi entre les populations: les morues du sud du golfe produisent presque 30 % de plus d'oeufs par unité de masse corporelle que celles du banc Georges, alors que la fécondité des morues de la plate-forme néo-écossaise est presque la moitié de celle des morues de la baie de Sydney. Par comparaison aux cycles biologiques des morues du banc Georges, les cycles des morues du sud du golfe se caractérisent par une forte fécondité, une maturation tardive, un indice gonadosomatique élevé et de gros oeufs. Par comparaison à l'influence de la taille, la condition physiologique, telle que reflétée par la masse du foie, l'indice hépatosomatique et le *K* de Fulton, n'explique ni les différences spatiales, ni les différences temporelles de la fécondité. La maturation tardive et une allocation plus importante dans la reproduction chez les morues du sud du golfe peuvent s'expliquer comme des réactions sélectives à une croissance plus lente, une mortalité pré-reproductive plus importante et un nombre plus limité d'occasions de reproduction durant la vie. Les patterns de covariation des caractéristiques héritables reliées au fitness font croire à une variation adaptative et à l'existence d'unités évolutives significatives à des échelles spatiales considérablement plus petites que l'aire de répartition de l'espèce dans le nord-ouest de l'Atlantique.

[Traduit par la Rédaction]

Introduction

Fundamental to life history theory is the assumption that natural selection favours those patterns of covariation in life history traits that maximise individual fitness. As such, fitness can be represented by *r*, the intrinsic rate of natural increase, and defined as either the rate of spread of an allele or the fitness of a genotype (Roff 2002). In population biology, *r* refers to the rate of growth over time of the number of individuals within the same population. From a conservation perspective, when a population has been considerably reduced in size, the time required for recovery to former levels of abundance depends on that population's maximum rate of increase, r_{max} (Hutchings 1999). Similarly, from a resource management perspective, r_{max} is positively correlated with sustainable rates of exploitation (Myers et al. 1997). Thus, the question of how fitness, as reflected by an individual's life history, affects population growth rate is of considerable interest.

To explain why population growth rates might differ, one requires an understanding of the adaptive and nonadaptive basis for life history trait variation within and among populations. One also requires information on the degree to which life histories differ through time and across space. In this regard, an issue of increasing importance to marine conservation biology concerns the degree to which widely distributed, broadcast-spawning marine fish exist as single populations

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throughout a given contiguous range or as smaller evolutionarily significant units (ESUs), reflecting adaptation to environmental conditions at smaller geographical scales (Waples 1998). Importantly, if individual life histories, and the population growth rates that they determine, differ at spatial scales smaller than those identified by resource management plans and species recovery programmes, it is unlikely that the objectives of these programmes will be realised.

Within this context, our work centres on describing and assessing the adaptive significance of temporal and spatial variation in the life history of Atlantic cod (*Gadus morhua*) from several stocks in the Northwest Atlantic: Southern Gulf of St. Lawrence (Northwest Atlantic Fisheries Organization (NAFO) division 4T); Sydney Bight (NAFO division 4Vn); Eastern Scotian Shelf (NAFO divisions 4Vs and 4W); and Georges Bank (NAFO division 5Ze) (Fig. 1). The spatial scale of our analysis corresponds to a level at which statistically significant genetic variability among cod has been reported. Differences in allelic variability at several microsatellite DNA loci have been documented between cod from Southern Gulf and Eastern Scotian Shelf (Ruzzante et al. 2000) and between cod from Eastern Scotian Shelf and Georges Bank (Ruzzante et al. 1998), lending credence to the premise that our life history comparisons have been made at a scale at which the genetic exchange of individuals appears to be relatively low. Also, the spatial scale of our analysis of Northwest Atlantic cod expands that encompassed by Pinhorn's (1984) study of temporal differences in size-specific fecundity of Newfoundland cod.

Among life history traits, we focus on size-specific fecundity and other metrics of reproductive investment, such as allocation of body tissue to gonads, age and size at maturity, and egg size. In addition to providing insights into cod life history variability across biologically meaningful scales, the potential utility of this work is reflected by arguments that direct metrics of fecundity may provide more accurate predictions of recruitment than spawner biomass (Marshall et al. 1998). Quantifying spatial differences in fecundity – body size regressions, for example, allows one to evaluate the degree to which geographical differences in recruitment might be attributable to differences in the number of eggs produced per individual during spawning, while controlling for potential effects of condition and body mass.

We also quantify population differences in Fulton's K and hepatosomatic index (HSI), metrics of physiological condition thought to be reliable proxies for the effect of environmental change on individual energy content and reproductive potential (Kjesbu et al. 1998; Marshall et al. 1999; Lambert and Dutil 2000). To test the veracity of this hypothesis, we examined whether Fulton's K, HSI, and liver weight are important determinants of size-specific fecundity within populations of cod in the Northwest Atlantic. We conclude by describing spatial patterns of life history trait covariation and assessing their adaptive significance.

Materials and methods

Collection of samples

Ovaries containing ripening eggs were examined from prespawning cod obtained from random samples of mature and immature fish captured from Northwest Atlantic waters encompassing the Canadian Maritime provinces (Fig. 1). Compared with preceding stages of maturity, ripening ovaries are larger, taking up more than one-half of the body cavity, and the oocytes are opaque and creamy yellow-orange in colour, because of the accumulation of yolk. Before release from the ovary, these oocytes are hydrated, giving them a transparent appearance. We excluded ovaries containing oocytes at this final stage of development, given the possibility that some may have already been spawned.

Ovaries containing ripening eggs were sampled from cod obtained by bottom trawl from randomly chosen locations throughout each management unit. Those from Eastern Scotian Shelf (n = 17 tows) and Georges Bank (n = 27 tows) were collected in February and March 1999 and 2000, during the annual groundfish research surveys conducted by the Canadian Department of Fisheries and Oceans (DFO). In the Southern Gulf of St. Lawrence, ovaries containing ripening eggs were collected in July 1998 and 1999 from random samples of cod (n = 23 tows) captured by fishermen engaged in a DFO-monitored Sentinel Fishery survey. Random samples from Sydney Bight were collected by one of us (T.M.M.) and by employees of the 4Vn Sentinel Fisheries Association from bottom-trawl surveys conducted under the auspices of the DFO, mainly in September of 1998 and 1999, with some samples obtained in July and August of both years (n = 34 tows).

All samples were labelled and frozen until processed in the lab, whereafter detailed measurements and otoliths were obtained. The former included total length (nearest centimetre) and total weight (nearest gram) for fish sampled from all areas and liver and ovary weights (nearest 0.1 gram) for fish collected in the Southern Gulf of St. Lawrence and Sydney Bight. Ages were determined from otoliths by experienced DFO staff in Moncton and St. Andrews, N.B., and in Dartmouth, N.S.

Estimation of fecundity and physiological condition

Following Buzeta and Waiwood (1982), ovaries were placed in glass jars containing Gilson's fluid (Snyder 1983), a chemical solution that degrades ovarian tissue without damaging oocytes. Jars were shaken periodically over a period of at least 12 weeks before ovarian tissue had been sufficiently degraded to allow for separation of the eggs. Ovaries too large to be fully contained in the glass jars were sectioned and weighed to the nearest 0.01 gram. For these samples, either one lobe of the ovary or the anterior portion of a lobe was excised from the entire ovary. Given that oocytes are homogeneously distributed throughout an ovary (Kjesbu 1988), the number of oocytes in one portion of an ovary should be comparable to the number of oocytes in another portion of an ovary of the same weight.

After the ovarian membrane and connective tissue had degraded to the extent that most oocytes were loose in the jars, the samples were washed through sieves of mesh sizes 1400 and 182 μm. The 1400-μm sieve retained most of the ovarian tissue, whereas the 182-μm sieve separated vitellogenic (mature) oocytes from previtellogenic (immature) oocytes. Our choice of mesh size was based on the Kjesbu et al.'s (1990) report that the onset of vitellogenesis occurs at an oocyte diameter of approximately 180 μm, an observation consistent with Morrison's (1990) description of cod gametogenesis.

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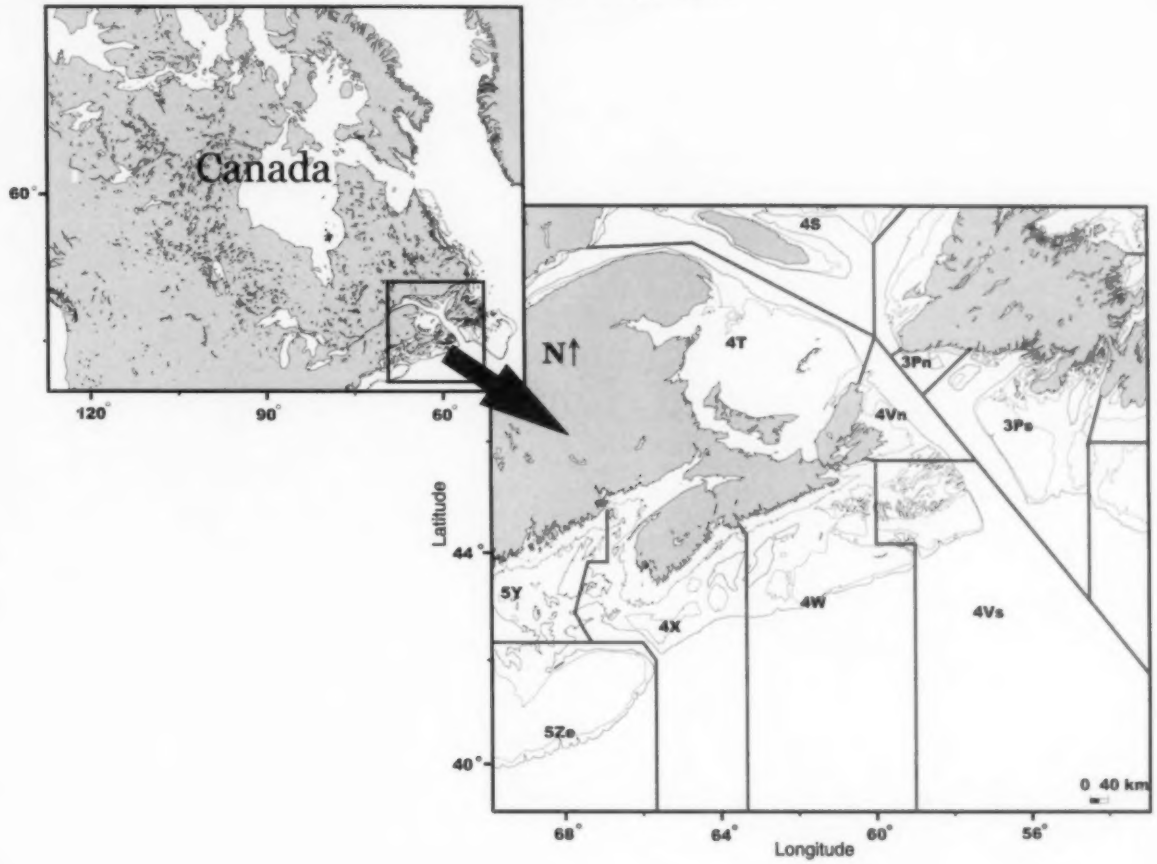
Fig. 1. Life history data were obtained from Atlantic cod (*Gadus morhua*) sampled from four Northwest Atlantic Fishery Organization (NAFO) management divisions: Southern Gulf of St. Lawrence (NAFO Division 4T), Sydney Bight (4Vn), Eastern Scotian Shelf (4Vs and 4W), and Georges Bank (5Ze). The solid lines delineate the 200-m depth contour.



This mesh size is considerably smaller than those used by Buzeta and Waiwood (1982; 250 μm) and by Powles (1957, 1958; 212 μm) in their studies of the fecundity of Southern Gulf cod sampled in 1980 and 1955–1956, respectively. To estimate the degree to which the larger mesh sizes would have underestimated fecundity, we compared the weight of eggs that passed through mesh sizes of 182 and 253 μm for 24 randomly chosen ovaries of Southern Gulf cod sampled in 1998 and 1999. On average, 3.6% of the eggs (by weight) in an ovary retained by the smaller mesh passed through the larger mesh. Given that these eggs would have been the smallest in each ovary, the numerical reduction in fecundity would have been greater than 3.6%. As a consequence, we will have underestimated any differences in size-specific fecundity between cod sampled in the late 1990s with those sampled decades earlier.

It is possible that our means of preserving the gonads (they were frozen before preservation in Gilson's fluid) could affect our estimates of size-specific fecundity. If freezing is more likely to damage the chorion of small eggs than large eggs and if Gilson's fluid is more likely to destroy small eggs than large eggs, then our absolute estimates of fecundity per unit body mass will have been underestimated. To our knowledge, such effects of freezing and Gilson's fluid on small eggs have not been documented in the primary literature. On the other hand, given that Gilson's fluid is known to slightly increase average egg size (Tanfermin 1991), any potential losses of small eggs may have been countered by an increase in estimated fecundity resulting from retention of eggs that, in a fresh state, would have passed through our 180-μm mesh. In any event, even if our preservation method did introduce a bias, it will not qualitatively affect our results given that any bias would have been consistent among all samples.

After each sample had been cleaned, vitellogenic oocytes were transferred to a known volume of water in a 4000-mL beaker and placed on a stirring plate above which a hand drill, with a stirring stick attached, was positioned. The magnetic stirrer was operated in one direction while the drill was operated in the reverse direction. The combination of the two devices increased the agitation of the mixture and minimized the effect of centrifugal force. When the oocytes appeared to be homogeneously distributed throughout the beaker, a 1- or 2-mL subsample was removed with a Stempel pi-

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pette. Oocytes in each of 3–5 subsamples per ovary were counted manually, using a binocular microscope.

Following Buzeta and Waiwood (1982) and Lambert and Dutil (2000), only those counts with a coefficient of variation (CV) of 10% or less were used in the data analysis. Fecundity (i.e., the number of vitellogenic oocytes) was estimated as

$$(1) \qquad F = F_{sub} \times V_{samp}/V_{sub} \times W_t/W_s$$

where F_{sub} is the mean number of eggs in subsample, V_{samp} is the volume (mL) of sample in the beaker, V_{sub} is the volume (mL) of subsample, W_t is the total weight (g) of ovaries, and W_s is the weight (g) of ovary section processed. A total of 233 ovaries, all of which were at the same stage of gonadal development, met our CV criterion. Adding the 47 samples from Powles' (1957, 1958) work and the 30 samples from Buzeta and Waiwood's (1982) study, data from a total of 310 ovaries were available for analysis.

Two condition indices and one metric of reproductive allotment were calculated for each fish. Fulton's K was calculated by dividing the somatic body weight (total body weight minus the gonad weight) by body length cubed and then multiplying by 100. The hepatosomatic index, HSI, was calculated by dividing liver weight by total body weight (to allow for comparison with other studies, acknowledging that some authors use somatic weight alone) and multiplying by 100. The gonadosomatic index, GSI, which reflects the proportional allocation of body tissue to the gonads, is equal to the ovary weight divided by total body weight and multiplying by 100 (Wootton 1998).

Statistical analysis

To model associations between fecundity and potential predictors of fecundity, we used a generalized linear model (GLM), incorporating a gamma response distribution coupled with a log-link function to connect the mean to the linear predictor(s) (Venables and Ripley 1998). In GLMs, the mean is modelled as a function of the covariates. As recommended by Venables and Ripley (1998), we used the gamma distribution to account for the increased variance in fecundity that we observed with increasing body size. The regression equation corresponding to this method, $Y = e^{ax+b}$, has a linear exponent. For some of the predictor variables examined here, for which no curvature in the fecundity data was observed across the range of explanatory variables, an identity link provided the best fit to the data. The regression equation corresponding to these GLMs was a simple linear expression, $Y = ax + b$. An analysis of covariance (ANCOVA) was used to test for annual differences in the slopes and intercepts of the fecundity – body size regressions within each population.

To assess the goodness-of-fit of each model, an analysis of deviance was used to identify the GLM that maximized the proportion of explained variation (PEV) in fecundity. To calculate the PEV, one compares the explained variation in the dependent variable before the addition of a predictor variable (null deviance) with the explained variation remaining in the model after the predictor variable has been added (residual deviance). The PEV for each fitted model is equal to (null deviance – residual deviance)/null deviance. Potential predictors of fecundity analysed here included body length, body weight, age, Fulton's K, liver weight, HSI, gonad weight, and GSI. Analyses of variance were used to test for differences in reproductive age, K, HSI, and GSI among populations. When appropriate, p values were corrected for multiple comparisons.

Results

Size at reproduction

The average size of Atlantic cod from which fecundity data were collected differed significantly among populations, being largest for cod on Georges Bank (79.4 ± 2.0 cm standard error, SE) and smallest for those on the Eastern Scotian Shelf (54.7 ± 1.8 cm) (Table 1).

Body size was the primary determinant of fecundity within the populations examined here, although the relative importance of size differed among years (Table 2). Of the two metrics of body size considered here, weight was generally a better predictor of fecundity than length. For Southern Gulf cod, weight explained 39% (1998 data) to 81% (1980 data) of the variation in fecundity. Weight also explained less variation in fecundity in 1998 for Sydney Bight cod (34%) than it did in 1999 (65%). Combining the 1998–2000 data for the relatively few (n = 29) mature cod sampled on Eastern Scotian Shelf, weight accounted for only 25% of the variation in fecundity. By comparison, weight accounted for large yet similar amounts of variation in fecundity for Georges Bank cod sampled in 1999 (77%) and 2000 (86%).

Temporal variation in fecundity–size relationships

To examine short- and long-term changes to size-specific fecundity within a single population, our fecundity data for Southern Gulf cod sampled in 1998 and 1999 were compared with those reported by Powles (1957, 1958) and by Buzeta and Waiwood (1982) for Southern Gulf cod sampled in 1955 and 1956 and in 1980, respectively. Both weight and length data were available for the 1980 cod, whereas only length data were reported for cod sampled in the 1950s. To ensure that cod of the same body sizes were compared in the ANCOVA, the weight range was limited to between 1800 and 8100 g, and the length range was limited to between 56 and 95 cm.

Size-specific fecundity of Southern Gulf cod differed over both short (2 years) and long (42–45 years) periods of time (Fig. 2). Although there was no significant difference in the slopes of either the fecundity–length and fecundity–weight regressions ($p > 0.6$ for all regressions), the ANCOVA indicated significant differences in the intercepts ($p < 0.0001$). Upon closer examination, the intercepts of the 1998 fecundity–size regressions were significantly less than those fitted to data for the other years (fecundity–length regression, $p < 0.01$; fecundity–weight regression, $p < 0.002$). Comparing the estimated fecundity for 70-cm cod (using the regressions presented in Table 2), Southern Gulf cod sampled in 1998 produced 775 000 eggs on average compared with 1.1 million eggs produced by the average 70-cm cod during the other time periods (1955–1956, 1980, 1999).

For cod inhabiting Georges Bank and Sidney Bight (there were insufficient data to undertake a temporal comparison for Eastern Scotian Shelf cod), neither the slopes nor the

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Table 1. Metrics of life history and physiological condition within four populations of Northwest Atlantic cod.

Population	Year	Length (cm)	Age (years)	GSI (%)	Fulton's K	HSI (%)	Relative egg size (mg)
Southern Gulf	1955–1956	81.7±3.1	8.8±0.4		—	—	—
		(n = 47)	(n = 44)				
	1980	73.4±3.1	—	11.7±0.7	0.90±0.02	—	0.34±0.03
		(n = 30)		(n = 30)	(n = 30)		(n = 30)
	1998	72.7±1.5	9.6±0.2	15.1±0.6	0.90±0.02	5.1±0.2	0.57±0.04
		(n = 35)	(n = 33)	(n = 35)	(n = 35)	(n = 35)	(n = 23)
	1999	60.7±2.6	7.4±0.3	13.0±0.9	0.86±0.01	3.3±0.4	0.50±0.04
		(n = 30)	(n = 30)	(n = 30)	(n = 30)	(n = 30)	(n = 27)
	All years	73.3±1.5	8.6±0.2	13.6±0.4	0.89±0.01	4.3±0.2	0.46±0.02
		(n = 142)	(n = 107)	(n = 95)	(n = 95)	(n = 65)	(n = 80)
Sydney Bight	1998	59.8±1.8	7.3±0.6	7.5±0.9	0.97±0.02	5.6±0.6	0.23±0.04
		(n = 27)	(n = 10)	(n = 26)	(n = 27)	(n = 27)	(n = 26)
	1999	58.1±1.9	7.5±0.6	6.7±0.5	0.89±0.03	4.3±0.4	0.17±0.02
		(n = 16)	(n = 15)	(n = 16)	(n = 16)	(n = 16)	(n = 16)
	All years	59.2±1.3	7.4±0.4	7.2±0.6	0.94±0.02	5.1±0.4	0.21±0.02
		(n = 43)	(n = 25)	(n = 42)	(n = 43)	(n = 43)	(n = 42)
Eastern Scotian Shelf	1998, 1999	55.3±4.2	8	8.1±1.1	0.76±0.02	2.9±1.0	0.30±0.06
		(n = 10)	(n = 1)	(n = 10)	(n = 10)	(n = 2)	(n = 9)
	2000	54.4±1.8	5.1±0.2	6.5±0.9	0.81±0.02	3.6±0.3	0.24±0.06
		(n = 19)	(n = 19)	(n = 19)	(n = 19)	(n = 7)	(n = 19)
	All years	54.7±1.8	5.2±0.2	7.1±0.7	0.79±0.02	3.4±0.3	0.26±0.04
		(n = 29)	(n = 20)	(n = 29)	(n = 29)	(n = 9)	(n = 28)
Georges Bank	1999	74.0±2.7	5.0±0.3	11.9±1.2	0.94±0.01	—	0.40±0.03
		(n = 56)	(n = 50)	(n = 55)	(n = 55)		(n = 49)
	2000	86.7±2.6	6.3±0.3	11.5±0.4	0.99±0.01	—	0.37±0.02
		(n = 41)	(n = 40)	(n = 41)	(n = 41)		(n = 41)
	All years	79.4±2.0	5.6±0.2	11.7±0.7	0.96±0.01	—	0.39±0.02
		(n = 97)	(n = 90)	(n = 96)	(n = 96)		(n = 90)

Note: GSI, gonadosomatic index (gonad weight/total body weight); K, somatic weight/length^3; HSI, hepatosomatic index (liver weight/total body weight). Data are means ± standard error.

intercepts of the fecundity–size regressions differed over the 2-year time periods for which data were available (Fig. 3).

Spatial variation in fecundity–size relationships

Size-specific fecundity differed significantly among Atlantic cod populations, as reflected by differences in the slopes and intercepts of the fecundity–size regressions. To examine spatial differences in fecundity by ANCOVA (using population as the factor variable), the yearly data were pooled for each population (the 1998 data were excluded for Southern Gulf cod given the aforementioned differences in the regression for this year). Given the significant effects of length on fecundity (Table 2) and to allow for inclusion of Powles' (1957, 1958) data, our spatial analysis was restricted to the fecundity–length relationships alone. The ANCOVA could not be used to compare all of the populations in a single analysis because the models that provided the best fit to the size and fecundity data did not have the same form for each population, being exponential for Southern Gulf and Georges Bank cod but linear for the Eastern Scotian Shelf and Sydney Bight populations.

Although there were no differences in regression slopes, significant differences in the intercepts of the fecundity–length regressions ($p < 0.01$) revealed differences in size-specific fecundity between the northern- and southern-most populations considered in our study. Comparing the estimated fecundity of 70-cm cod, size-specific fecundity of Southern Gulf cod (1.1 million eggs) was 27% higher than that estimated for Georges Bank cod (866 000 eggs). By contrast, the slopes of the fecundity–size regressions for Eastern Scotian Shelf and Sydney Bight cod differed from one another, the rate at which fecundity increased with length being greater for Sydney Bight cod than for cod on Eastern Scotian Shelf.

Age at reproduction

The average age of fish from which ripe ovaries were sampled tended to decline with latitude (Table 1). For cod sampled between 1998 and 2000, the youngest age at reproduction declined from 5 and 4 years for Southern Gulf and Sydney Bight cod, respectively, to 3 and 2 years for cod on Eastern Scotian Shelf and Georges Bank, respectively. Comparing the mean age of reproductive cod from the northern- and southern-most populations examined here, Georges Bank females were significantly younger (5.6 ± 0.2 years) than those in the Southern Gulf (8.6 ± 0.2 years) ($p < 0.001$). Similarly, the incidence of reproduction among cod younger than 5 years was 36.7% among Georges Bank females compared with <1% for Southern Gulf cod.

Although age had lower explanatory power than either body length or weight, it did account for a significant amount of variation in fecundity in three of four populations, ex-

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Table 2. Regression model parameter estimates for fecundity–size relationships within four populations of Atlantic cod.

Population	Year(s)	*n*	Size variable	Model	Slope	Intercept	PEV	*p*
Southern Gulf	1955, 1956	47	Length	E	0.036	11.52	0.70	<0.0001
	1980	30	Weight	E	0.0002	13.02	0.81	<0.0001
			Length	E	0.046	10.86	0.78	<0.0001
	1998	35	Weight	E	0.0003	12.59	0.39	0.0001
			Length	E	0.043	10.55	0.37	<0.0001
	1999	30	Weight	E	0.0004	12.23	0.66	<0.0001
			Length	E	0.060	9.66	0.71	<0.0001
	1980, 1999	60	Weight	E	0.0003	12.62	0.72	<0.0001
	1955, 1956, 1980, 1999	107	Length	E	0.044	10.83	0.73	<0.0001
Sydney Bight	1998	27	Weight	L	346.64	11 099	0.34	0.0018
			Length	L	36 530	–1 362 418	0.38	0.0005
	1999	16	Weight	L	393.04	28 035	0.65	<0.0001
			Length	L	37 625	–1 400 390	0.63	0.0002
	1998, 1999	43	Weight	L	352.93	38 127	0.39	<0.0001
			Length	L	36 983	–1 379 115	0.43	<0.0001
Eastern Scotian Shelf	1998–2000	29	Weight	L	240.86	83 046	0.25	0.0038
			Length	L	16 517	–466 525	0.28	0.0025
Georges Bank	1999	55	Weight	L	321.24	–143 687	0.77	<0.0001
			Length	E	0.056	9.70	0.73	<0.0001
	2000	41	Weight	L	340.44	–94 437	0.86	<0.0001
			Length	E	0.042	11.00	0.82	<0.0001
	1999, 2000	96	Weight	L	336.03	–153 199	0.80	<0.0001
			Length	E	0.052	10.03	0.75	<0.0001

Note: E, exponential model ($Y = e^{ax+b}$); L, linear model ($Y = ax + b$); PEV, percentage explained variation.

plaining 23% ($p < 0.0001$), 26% ($p = 0.006$), and 53% ($p < 0.0001$) of the variation in fecundity for Southern Gulf, Sydney Bight, and Georges Bank cod, respectively.

Effects of condition on fecundity

Physiological condition, as reflected by Fulton's *K* and the hepatosomatic index (HSI), differed by varying degrees within and among populations. For the Southern Gulf, the only population for which a long-term temporal comparison was possible, Fulton's *K* did not differ significantly among cod sampled in 1980, 1998, and 1999 (Table 1). However, significant differences were evident among populations ($p < 0.001$), being lowest for Eastern Scotian Shelf cod (0.79 ± 0.02) and highest for cod on Georges Bank (0.96 ± 0.01). Comparing the relative size of the livers, the HSI of Southern Gulf cod was significantly lower in 1999 (the year of higher size-specific fecundity) than it was in 1998 ($p < 0.0001$), although there were no differences in HSI for Sydney Bight cod between the same years.

To examine the effects of condition on egg number per female, Fulton's *K* and HSI were added separately to the fecundity – body size GLM regressions to determine whether they explained a significant amount of variation in fecundity additional to that attributed to body length or weight alone. Georges Bank was the only population for which Fulton's *K* explained a significant amount of variation in fecundity in addition to that explained by body size (length). However, although the statistical significance was high ($p < 0.0001$), biologically the increase in explained variation was only 3% above the 75% explained by length alone. Notably, the amount of variation in fecundity explained by weight alone (80%) in Georges Bank cod exceeded the combined variation explained by length and Fulton's *K*.

In general, neither the proportional nor absolute weights of the liver were correlated with fecundity. The HSI, measured at the time of spawning, was not significantly associated with fecundity within either of the two years during which cod were sampled from the Southern Gulf and Sidney Bight. To assess the potential influence of HSI several months before spawning, we examined data on liver weights obtained for 18 Southern Gulf cod of sizes similar to those sampled during the summer of 1999, caught in the autumn of 1998 by the Department of Fisheries and Oceans (G. Chouinard, Department of Fisheries and Oceans, P.O. Box 5030, Moncton, NB E1C 9B6, Canada, personal communication). Although HSI from cod sampled in September 1998 was significantly related to the fecundity of cod sampled the following July, the PEV (0.21) for this fecundity–HSI relationship was much less than the variation explained by weight and length alone in 1999 (0.66 and 0.71, respectively). When the HSI for cod sampled in September 1998 was added to the fecundity–weight and fecundity–length models for cod sampled in 1999, the increase in PEV was not statistically significant.

When either body weight or length was combined with liver weight as predictors of fecundity for Sydney Bight and Southern Gulf (1999) cod, the explained variation did not increase significantly beyond the PEV of fish weight or length alone ($p > 0.39$). Liver weights of Southern Gulf cod sampled in 1998 explained marginally more variation in fecundity (identity link model: PEV = 0.44) than either fish length (PEV = 0.37) or fish weight (PEV = 0.39) alone; addition of fish length or weight to the fecundity – liver weight model

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Fig. 2. Associations between log(fecundity) and (*a*) body length and (*b*) total body weight for female Atlantic cod (*Gadus morhua*) in the Southern Gulf of St. Lawrence. In Fig. 2*a*, the solid line represents data pooled from 1955, 1956, 1980, and 1999 and the broken line represents data from 1998 only. In Fig. 2*b*, the solid line represents data pooled from 1980 and 1999 and the broken line represents data from 1999 only. Symbols: squares, 1955 and 1956; circles, 1980; triangles, 1998; crosses, 1999.

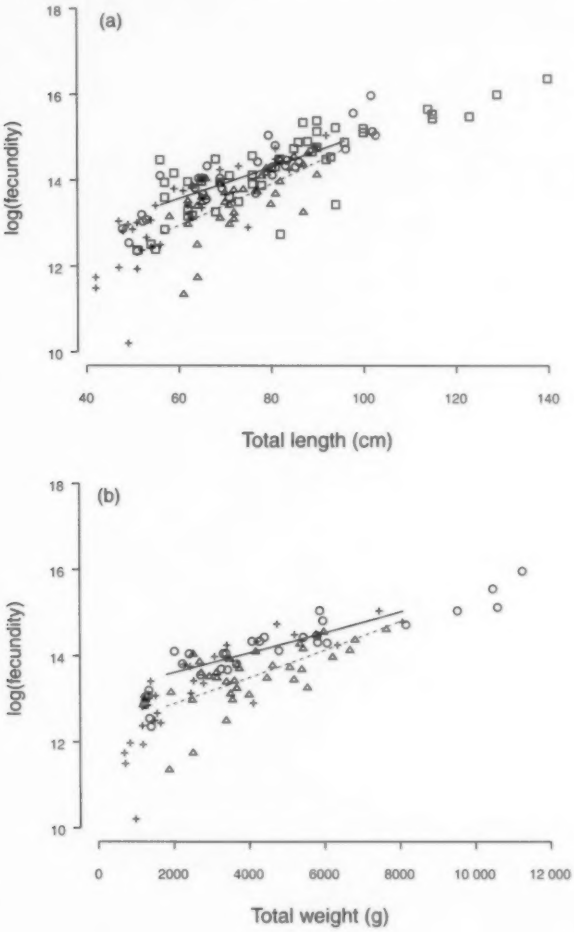
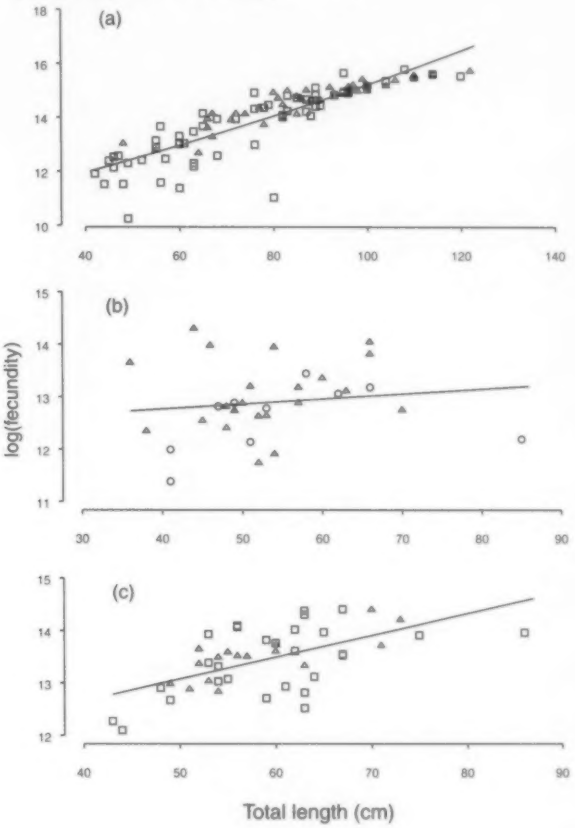


Fig. 3. Associations between log(fecundity) and total body length within three populations of female Atlantic cod (*Gadus morhua*): (*a*) George Bank (squares, 1999; triangles, 2000); (*b*) Eastern Scotian Shelf (circles, 1998 and 1999; triangles, 2000); (*c*) Sydney Bight (squares, 1998; triangles, 1999).



did not significantly increase the amount of explained variation ($p > 0.05$).

Gonadosomatic index

The proportional allocation of body tissue to the gonads, for individuals whose ovaries were at the same developmental stage, differed significantly among years in the Southern Gulf of St. Lawrence and among populations in the Northwest Atlantic (Table 1). Within the Southern Gulf, the average GSI of cod sampled in 1998 (15.1 ± 0.6%) was significantly ($p = 0.0007$) greater, despite having a lower size-specific fecundity, than that of cod sampled in 1980 (11.7 ± 0.7%). Among populations, the GSI was lowest for Eastern Scotian Shelf (7.1 ± 0.7%) and Sydney Bight cod (7.2 ± 0.6%), which corresponded with their lower size-specific fecundity at the population level. Comparing cod from the northern- and southern-most populations, the GSI of Georges Bank cod (11.7 ± 0.7%) was significantly ($p < 0.001$) lower than that of cod sampled from the Southern Gulf (13.6 ± 0.4%) (Table 1). Controlling for body size and parity (approximated by the potential number of annual reproductive events), GSI was higher for Southern Gulf cod than it was for cod on Georges Bank (Fig. 4)

When used as a predictor of fecundity in the generalized linear model, GSI was significantly related to fecundity only for cod on Georges Bank (PEV = 0.205; $p < 0.0001$). However, fish weight alone explained much more variation in the model than GSI, and the addition of GSI to the fecundity – fish weight model did not significantly increase the PEV of the model ($p > 0.2$). Although ovary weight was significantly associated with fecundity in all areas (PEV ranging between 0.21 and 0.68; $p < 0.004$) except Eastern Scotian Shelf ($p = 0.50$), the amount of variation in fecundity ex-

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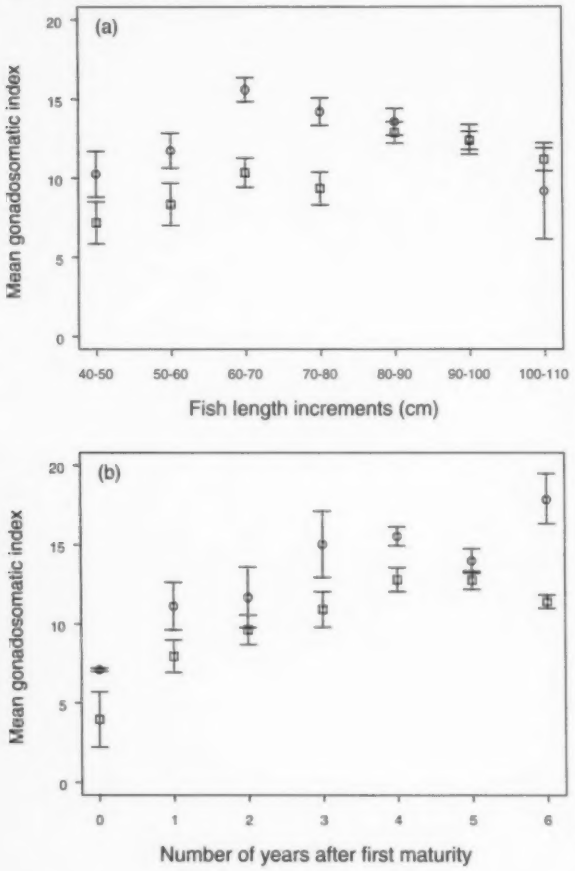
Fig. 4. Gonadosomatic index ((gonad weight/total body weight) × 100%; ±1 standard error) of female Atlantic cod (*Gadus morhua*) on Georges Bank (squares) and Southern Gulf of St. Lawrence (circles) as functions of (*a*) total body length and (*b*) number of years after the earliest observed age at reproduction within each population.



plained by ovary weight was always less than that explained by body weight or body length alone.

Egg size

Average relative egg size per female was measured by dividing total ovary weight by egg number within females with ovaries at the same stage of development (see Materials and methods), a calculation that will underestimate actual egg weight because of the inclusion of unknown amounts of gonadal tissue in the numerator. Relative egg size differed significantly among populations ($p < 0.001$), being smallest for Scotian Shelf and Sydney Bight cod (Table 1). Comparing the northern- and southern-most populations, Southern Gulf cod produce significantly larger eggs than cod from Georges Bank cod ($p = 0.014$).

Discussion

Life histories of Northwest Atlantic cod differ at relatively small scales through time and space. Within the Southern Gulf population, average fecundity per unit body mass varied significantly over short (2 years) and long (42–45 years) periods of time, differing by more than 40% among years. Indeed, given that the mesh size used to separate the relatively large vitellogenic oocytes from the smaller previtellogenic oocytes was smaller than those used in previous work (Powles 1957, 1958; Buzeta and Waiwood 1982), the reduction in size-specific fecundity that we document here for Southern Gulf cod in the late 1990s, relative to that recorded decades earlier, has almost certainly been underestimated. Spatially, significant variation in size-specific fecundity was also evident among populations. Southern Gulf cod produce almost 30% more eggs per unit body mass than those on Georges Bank, whereas the fecundity of Eastern Scotian Shelf cod is about half that of cod in Sydney Bight. In general, relative to the influence of body size, neither temporal nor spatial differences in fecundity can be attributed to individual differences in physiological condition, as reflected by the hepatosomatic index and Fulton's *K*. However, patterns of covariation in several life history traits (including age and size at maturity, reproductive allotment, egg size, and growth rate) are consistent with those predicted by life history theory. We suggest that spatial differences in heritable fitness-related traits among cod populations, previously demonstrated to be genetically distinguishable, is consistent with the hypothesis of adaptation to local environments.

Temporal variation in size-specific fecundity

The substantive temporal differences in fecundity documented here for Southern Gulf of St. Lawrence cod appear to be similar to those documented elsewhere. For females 70 cm in length, size-specific fecundity differed 42% between the two time periods for which significant differences in length–fecundity regressions existed (period 1, 1998; period 2, 1955/1956, 1980, 1999). Based on fecundity estimates presented by Marteinsdottir and Begg (2002) for 70-cm cod, the temporal difference reported here for Southern Gulf cod might in fact be deemed low, given the 106% and 76% annual differences reported for Icelandic and Northeast Arcto-Norwegian cod, respectively. However, these latter two percentages may unduly overestimate temporal variability in size-specific fecundity within these populations, given that the years in which fecundity–length regressions did not differ from one another was not reported for either of these stocks. For example, even though there was no statistical difference between the Southern Gulf cod fecundity–length regressions for the years 1955–1956, 1980, and 1999, the estimated fecundity of a 70-cm cod ranged between 1.045 million and 1.303 million eggs. Using the high annual estimate of 1.303 million and comparing it with the estimate for 70-cm cod in 1998 (775 000), one would have concluded that size-specific fecundity differed 68%, rather than the more statistically defensible 42%, among years.

We are unable to identify the specific environmental factors responsible for temporal differences in size-specific fecundity of Southern Gulf cod. Although water temperature has been implicated as contributing to temporal and spatial variability in fecundity among cod off Newfoundland (Pinhorn 1984) and in the Baltic (Kraus et al. 2000), temperatures in the Southern Gulf did not differ appreciably between 1998 and 1999 (Drinkwater et al. 2001). Nonetheless,

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it is important to recognise that such short-term variability in size–fecundity can exist (Marteinsdottir and Begg 2002; present study) and that population demography is likely to be affected as a result. The potential consequences of such interannual variability in reproductive allotment to recruitment underscores the importance of quantifying the effects of fecundity on year-class strength (Marshall et al. 1999; Köster et al. 2000) and draws attention to a potential source of nonstationarity in stock–recruitment relationships (Walters and Korman 2001).

Causes of temporal variation in size-specific fecundity: a critique

With one exception (liver weight explained 5% more variation in fecundity than body weight among Southern Gulf cod in 1998), body size was the best predictor of fecundity within all populations, explaining significantly more variation than age, Fulton's *K*, HSI, liver weight, and ovary weight, none of which significantly increased the explained variation in fecundity when included in either fecundity–length or fecundity–weight regression models.

Although it is not unreasonable to expect metrics of condition to be associated with fecundity, it is important that one be able to distinguish the statistical, and biological, influence of these metrics on female egg number from the effect of body size alone. Kjesbu et al. (1998), for example, reported that liver weight, when added as an explanatory variable to a fecundity–length regression for Northeast Arctic cod, contributed significantly to fecundity. Yet the variation in fecundity explained by both of these variables (r^2 = 0.93) was not significantly greater than that explained by fish length alone (r^2 = 0.92) and was less than that explained by fish weight alone (r^2 = 0.94). In a laboratory study of Northern Gulf of St. Lawrence cod, Lambert and Dutil (2000) reported that Fulton's *K*, measured at the time of spawning, accounted for 14–23% of the variation in fecundity and egg dry weight in addition to the 49–51% explained by length alone. Unfortunately, these authors did not report the variation in fecundity accounted for by body weight alone, which often explains more of the variation in fecundity than length (Wootton 1998), nor did they account in their regression models for the fact that *K* and length are not independent of one another, thus inflating the variation in fecundity explained by *K* (a statistical deficiency common to much of the work in this area). Recently, Marteinsdottir and Begg (2002) reported a statistically significant influence of HSI on fecundity in Icelandic cod. Although they did not report the explained variance in fecundity attributable to HSI, based on their sums of squares table (table 6 in Marteinsdottir and Begg 2002), it appears that liver condition explained 3%, or less, of the variation in fecundity in addition to that explained by body size alone.

We do not wish to suggest that condition does not influence fecundity. As decades of life history research have revealed, the existence of physiological precursors to, and costs associated with, reproduction is one of the fundamental premises of life history theory (Wootton 1998; Roff 2002). However, the present study does raise questions concerning the ubiquity of condition effects on fecundity, the degree to which field data can be used to quantify accurately such effects, the biological and environmental conditions under which such effects might be most evident, and the influence of condition on fecundity per se relative to its effect on other facets of reproduction, such as behaviour.

As noted above, the lack of influence noted here may reflect the difficulty in determining the time of year, or indeed the age, at which the effect of body condition on fecundity is greatest. For example, based on field data collected by Eliassen and Vahl (1982), condition may have its greatest effect on fecundity 4–6 months before spawning, the period when cod are accumulating energy before reproduction. Also, just before spawning, cod ovaries contain oocytes that will be spawned in both the current and subsequent spawning seasons (Kjesbu et al. 1990), suggesting that the number of oocytes produced each year is determined at least 1 year, and possibly 2 years, before reproduction. In addition, failure to detect a strong influence of condition on fecundity would not be surprising if the proportional allocation of a female's gonads to present and future spawning events differed within and among populations (which it almost certainly does). Thus, any effect of condition on fecundity may be greatest not during the current spawning season but on subsequent spawning seasons (Kjesbu et al. 1996; Schwalme and Chouinard 1999).

In addition to the interpretive and inferential limitations raised above, lack of association between condition and fecundity may reflect a diminishing effect of condition above some threshold level, indicative of an asymptotic association between fecundity and condition. If so, a biologically relevant influence of condition on fecundity would not be realised unless condition fell below that threshold. Based on recruitment data for Northeast Arctic cod reported by Marshall et al. (1999), such a threshold for HSI may be approximately 6%. However, we note that the HSI values for Southern Gulf and Sydney Bight cod in 1998 and 1999 (ranging from 3.3% to 5.6%) were all below this threshold estimate. Although Marshall et al.'s (1999) data were averages of monthly values for a particular length class of cod, their findings lead us to conclude that the range in HSI documented here should have been within the range at which HSI might be predicted to have its strongest influence on fecundity.

Notwithstanding the apparent lack of influence of condition on fecundity reported here and elsewhere (Ma et al. 1998; Kraus et al. 2000), condition may still be an important determinant of recruitment (Marshall et al. 1999). But rather than affecting the number of eggs that a female produces, the primary effect of condition on offspring production may well be realised through spawning behaviour. This is supported by the observation that more than half of the lipid losses resulting from reproduction can be attributed to nongonadal tissues in the few fishes for which such an effect has been examined, e.g., Atlantic salmon, *Salmo salar* (Jonsson et al. 1991), and brook trout, *Salvelinus fontinalis* (Hutchings et al. 1999).

Adaptive significance of spatial differences in life history trait covariation

Northwest Atlantic cod life histories differ significantly across relatively small geographic scales. Based on the data presented here for cod inhabiting the waters of the Southern Gulf, Sidney Bight, Eastern Scotian Shelf, and Georges Bank, population differences in life history are reflected by among-

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population variation in age and size at maturity, reproductive allotment, fecundity, egg size, and individual growth rate, fitness-related traits known to be heritable in fishes (Wootton 1998; Roff 2002).

A comparison of cod from the southern and northern geographical limits of the present study reveals consistent patterns of covariation in several life history traits. Relative to females in the Southern Gulf, Georges Bank cod mature earlier in life, produce fewer and smaller eggs per unit of body mass, and allocate proportionately less of their body tissue to gonads. But despite maturing at considerably different ages, there are few differences in size at maturity between populations. Based on data collected in the present study, minimum size at maturity was equal (42 cm), as were the 25% quartile lengths at reproduction (62–63 cm), suggesting that Georges Bank cod experience significantly faster rates of growth than Southern Gulf cod.

These patterns of trait covariation are consistent with expectations based on life history theory; as such, they can be explained as adaptive responses by cod to their local environments. Compared with Georges Bank females, Southern Gulf cod take longer (about 3 years longer) to reach a size at which reproduction is possible, because of their slower growth rate, meaning that Southern Gulf cod almost certainly experience higher cumulative mortality than Georges Bank cod during the prereproductive phase of life. All else being equal, once Southern Gulf cod reach maturity, their probability of survival to death will be less than that for Georges Bank cod. In response to this higher mortality before reproduction and to an expected fewer number of lifetime reproductive events, theory would predict that Southern Gulf cod would expend greater reproductive effort during spawning (Roff 2002), a prediction borne out by higher size-specific fecundity and GSI.

Based on a series of recent geographical comparisons of fitness-related traits in north temperate marine fish, it is becoming evident that adaptive variation can exist at spatial scales considerably smaller than previously thought. For Northwest Atlantic cod, genetic differences have been documented in growth rate and food conversion efficiency (Purchase and Brown 2001), in antifreeze proteins (Goddard et al. 1999), and in the influence of light intensity on growth and survival in early life (Puvanendran and Brown 1998). Among Northeast Atlantic marine fishes, such as Atlantic halibut (*Hippoglossus hippoglossus*) and turbot (*Scophthalmus maximus*), there is similar evidence for genetic differences in growth rate and feeding efficiency among geographically disparate populations (Imsland et al. 2000; Jonassen et al. 2000).

Differences in Atlantic cod life history can be expected to manifest themselves at the population level as differences in r_{max}, the parameter of primary importance when assigning sustainable rates of harvest and when evaluating the conservation status and extinction probability of depleted populations (Hutchings 2003). The finding that life histories can vary across relatively small geographical scales is germane to the issue of whether evolutionarily significant substructuring exists among Atlantic cod populations in the Northwest Atlantic. Given that significant genetic differences have been detected among Atlantic cod populations at spatial scales similar to, or smaller than, those of the present study (Ruzzante et al. 1998; Pogson et al. 2001), the patterns of covariation among heritable traits documented here are consistent with the hypothesis that this species exists in the Northwest Atlantic as multiple, locally adapted populations at spatial scales considerably smaller than the range of the species. The challenge to marine population ecologists and geneticists will be in delineating these population boundaries.

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Detecting juvenile survival effects of habitat actions: power analysis applied to endangered Snake River spring–summer chinook (*Oncorhynchus tshawytscha*)

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Abstract: Using 10 years of parr-to-smolt survival rate estimates for passive integrated transponder (PIT) tagged, endangered wild Snake River chinook (*Oncorhynchus tshawytscha*) (measured in eight spawning streams), we demonstrate that moderate increases in base-case survival may be detectable quickly, as required by recent U.S. National Marine Fisheries Service regulations. The regulations require that effects of tributary habitat actions on juvenile salmonid survival rates be detectable within 5 to 8 years. Simple log-linear regression models were employed where the natural log of survival is a function of parr size, parent stock abundance, tagging location, and year. The analysis uses before–after control–impact (BACI) statistical techniques. The results suggest that multiplicative survival rate changes of 30% should be detectable within 7 years, and increases of 50% within 3 years. Models with higher information-theoretic weights were more powerful than less plausible models. Models using juvenile survival were substantially more powerful than models using spawner–recruit data for the same stocks, but the analysis is no substitute for field studies, which are still very rare.

Résumé : Sur une période de 10 ans et dans 8 cours d'eau de fraye, des estimations de la survie des tacons jusqu'au stade saumoneau chez les saumons quinnat (*Oncorhynchus tshawytscha*) sauvages menacés de la rivière Snake, munis d'émetteurs PIT (transpondeurs passifs intégrés) nous a permis de démontrer que des accroissements modérés dans la survie de base peuvent être détectés rapidement, comme l'exigent les nouveaux règlements du U.S. National Marine Fisheries Service. Ces règlements requièrent que les effets des modifications des habitats des tributaires sur les taux de survie des jeunes saumons soient décelables dans les 5 à 8 ans suivants. Des modèles logarithmiques linéaires simples ont été utilisés dans les cas où le logarithme naturel de la survie est fonction de la taille des tacons, de l'abondance des stocks des reproducteurs, du site de marquage et de l'année. Notre analyse utilise des techniques statistiques de type BACI (avant–après, témoin–impact). Les résultats indiquent que des changements multiplicatifs dans les taux de survie de l'ordre de 30 % devraient être détectables en moins de 7 ans et des changements de 50 % en moins de 3 ans. Les modèles qui incluent plus d'information et de théorie sont plus puissants que les modèles moins plausibles. Les modèles qui utilisent la survie des jeunes sont considérablement plus puissants que les modèles du même stock basés sur des données concernant les reproducteurs et les recrues; l'analyse ne peut, cependant, remplacer les travaux de terrain qui restent encore très rares.

[Traduit par la Rédaction]

Introduction

A recent U.S. National Marine Fisheries Service (NMFS) Biological Opinion on Endangered Species Act listed chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) requires that Bonneville Power Administration (BPA) and the U.S. Army Corps of Engineers increase survival rates for juvenile salmon and steelhead rearing in tributaries (NMFS 2000). It also requires that the agencies demonstrate that egg-to-adult survival rates have increased and do so in a manner that is statistically defensible. Given substantial past expenditures on habitat modifications in salmonid spawning and rearing areas, one might think that many examples would be available in the literature to demonstrate likely changes in survival rates and experimental designs to detect these changes. However, this is unfortunately not the case. For example, a recent literature survey of over 2000 references (Bayley 2002) uncovered only a handful of studies that used statistically rigorous experimental designs to demonstrate the effects of habitat modifications on salmonid survival. Roni et al. (2003) found some studies relating changes in juvenile abundance to changes in local habitat

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conditions, but these do not really answer the question posed by NMFS — do habitat actions cause measurable increases in juvenile salmonid survival rates?

Recent work by Paulsen and Hinrichsen (2002) used over 40 years of spawner–recruit estimates for seven endangered Snake River spring–summer chinook (*Oncorhynchus tshawytscha*) stocks in a variety of power analyses. We found that if juvenile life-stage survival were doubled for four of the stocks (with the other three stocks as untreated controls), one could detect the survival change after 3 to 4 years of the treatment, with type I error (α) of 5% and power of 80%. However, because juvenile survival increases would not become apparent for 4 to 5 years (when mature adults return to spawn), 8 to 10 years would be required to complete the experiment. In addition, it may take decades for smaller changes in juvenile survival to manifest themselves via changes in spawner returns (C.M. Paulsen and R. Hinrichsen, unpublished data).

In other recent work (Paulsen and Fisher 2001), we found that survival rates of Snake River spring–summer chinook (passive integrated transponder (PIT) tagged in upper tributaries as parr in the summer and fall and then detected as seaward migrating smolts the following spring at the mainstem Snake River and Columbia River hydropower dams) were related to indices of land use and land cover, climate (the Palmer drought severity index (PDSI)), length of the parr at the time of tagging, and (for some models) month of tagging. We suspected that juvenile survival estimates for the index stocks analyzed in Paulsen and Hinrichsen (2002) might be a more powerful measure of survival changes caused by tributary habitat actions. Because increases in parr-to-smolt survival, the dependent variable in the current analysis, would be measurable within a year, there is no need to wait for the affected fish to return as adults. However, it is possible that the increases may not carry through to adult returns owing to density dependence or other causes.

In this analysis, we consider trade-offs among the regression models used in the power analysis (more plausible models may be more powerful), the number of treatment sites, the length of the experiment (i.e., the number of treatment years), and the effect size (i.e., the multiplicative increase in the parr-to-smolt survival rate). The objective is to show how many years and treatment sites would be required to detect a given effect by rejecting the null hypothesis that the estimated effect size is zero. For brevity, several other variables or decision criteria are assumed to be constant for this analysis, including (*i*) the acceptable level of error (α, assumed to be 5%, and acceptable power, assumed to be 80%), (*ii*) whether a one- or two-tailed test is used (a two-tailed test was used to allow for the possibility that purportedly beneficial modifications may in fact reduce survival rates), (*iii*) the number of fish tagged and hence the precision of annual estimates of survival for a given stream or site (assumed to be the same as in the past), and (*iv*) the detection probability at mainstem Snake River and Columbia River dams (also assumed to be the same as in past years).

The power analysis is just one part of a comprehensive experimental design. Such a design would include careful selection of treatment and control sites, educated guesses regarding effect sizes, coordination with organizations doing the actual habitat modifications, monitoring of physical and environmental variables, and many other factors not addressed here.

Data

Because the data and estimates of survival for tagged parr are an extension of those developed in Paulsen and Fisher (2001), we briefly summarize the methods used therein and present updated estimates of survival and the other variables used in the power analyses. We then describe the independent variables that we used.

Since the late 1980s, BPA and NMFS have sponsored PIT tagging studies on Snake River origin salmon and steelhead populations. In late summer and early autumn, age-0 wild spring–summer chinook salmon parr (progeny of the previous year's spawners) are collected, tagged, and returned to their natal streams. These rearing areas are headwater streams and small rivers in Idaho and Oregon upstream from Lower Granite Dam (LGR), the uppermost dam on the Snake River through which these stocks migrate as adults and juveniles. For comparison with the index stocks used in Paulsen and Hinrichsen (2002), we utilized data on eight stocks (Fig. 1 and Table 1). Each of the PIT tags implanted in the parr has a unique serial number (Achord et al. 1997). Therefore, subsequent capture histories for each fish can be recorded at detectors installed in the juvenile bypasses at mainstem hydroelectric dams and are available for download from the Columbia Basin PIT Tag Information System (PTAGIS; PSMFC 2002). The following spring (from roughly April through June), the tagged smolts are detected at LGR, Lower Monumental, and Little Goose dams on the lower Snake River and McNary, John Day, and Bonneville dams on the lower Columbia River as they migrate to the Pacific Ocean. Survival from tagging to LGR can be estimated from the numbers of fish released at upstream locations and recaptured at the dams (Smith et al. 1994; Paulsen and Fisher 2001).

We used eight sites corresponding to the seven index stocks in Paulsen and Hinrichsen (2002), with Bear Valley Creek and Elk Creek being treated as separate sites or stocks in this analysis. A total of approximately 141 000 parr were tagged by numerous organizations (NMFS, Idaho Department of Fish and Game (IDFG), Oregon Department of Fish and Wildlife (ODFW), and the Nez Perce Tribe Department of Fisheries (NPT)) at these eight sites from 1992 through 2001. Because each site was not visited in every year (owing to low spawning abundance in some years and logistical problems), the result is 65 site–year combinations or observations in the resulting data set versus 80 if fish had been tagged at all sites in every year.

The fish from each site–year were then placed into five mutually exclusive categories: (1) never seen after release; (2) seen only at LGR and returned to the river; (3) seen only at dams downstream from LGR; (4) seen at both LGR and one or more downstream dams; and (5) transported at LGR to below Bonneville Dam. The counts for fish released from each site and year were then used to estimate the proportion of fish surviving from tagging in the spawning streams each summer to LGR the following spring. Details on our maximum likelihood estimates of survival rates can be found in Paulsen and Fisher (2001).

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Fig. 1. Tagging sites (fish icon) and overwintering areas for the eight passive integrated transponder (PIT) tagged Snake River spring–summer chinook (*Oncorhynchus tshawytscha*) stocks and location of the mainstem hydropower dams where tagged smolts are detected. Degrees latitude and longitude are shown in each corner of the figure. Inset map shows location in the Columbia River basin (northwestern U.S.A.).

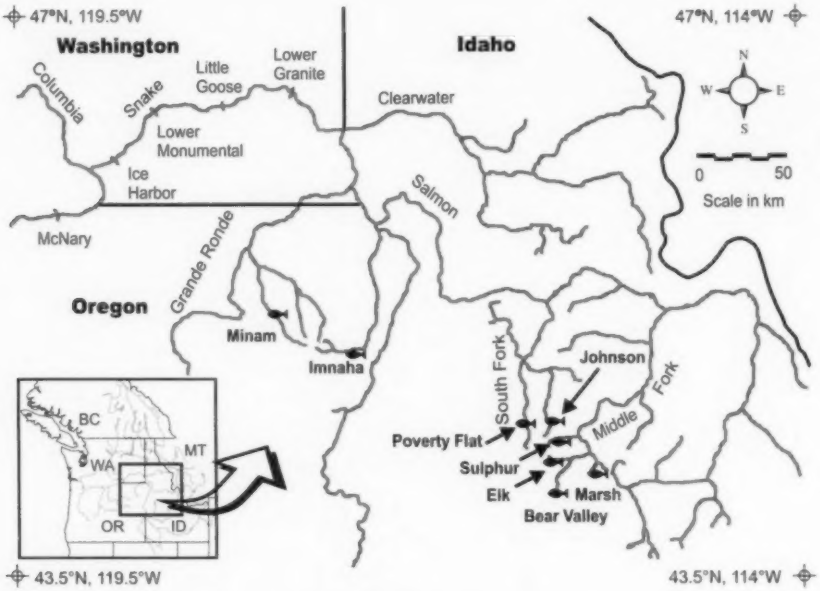

Table 1. Tagging sites, climatic regions, land use–cover categories.

Tagging site	Region	Land use–cover category
Bear Valley Creek	Middle Fork Salmon River	Wilderness
Elk Creek	Middle Fork Salmon River	Wilderness
Imnaha River	Northeast Oregon	Transitional
Johnson Creek	South Fork Salmon River	Older dry forest
Marsh Creek	Middle Fork Salmon River	Wilderness
Minam River	Northeast Oregon	Wilderness
Poverty Flat	South Fork Salmon River	Older dry forest
Sulphur Creek	Middle Fork Salmon River	Wilderness

The number of fish tagged, number of sites where tagging occurred, proportions detected at LGR, and the natural log of survival are all highly variable, both among sites and over time (Fig. 2). The number of sites varies from three to eight, whereas the number of parr tagged varies by an order of magnitude, from about 2500 to 25 000 (Fig. 2*a*). Detection rates for smolts passing LGR vary as well, from about 15% to 85% (Fig. 2*b*). The means, minima, and maxima for the natural log of the estimated survival rates also vary widely (Fig. 2*c*).

The tagging sites and region for each site are used as classification or dummy variables in the regression models (Table 1). The land-use categories are taken from Paulsen and Fisher (2001). Because five of the eight sites are in wilderness areas, these five are always used as control sites in the power analysis; chinook emigrating from wilderness areas had the highest survival of the land-use categories considered in Paulsen and Fisher (2001). The land-use categories were not used directly in the current analysis, as the number of sites and categories is quite limited. One other variable used in Paulsen and Fisher (2001) but not used here is month of tagging, as the earlier work did not find a consistent relationship between month and survival (perhaps because it is correlated with length, as parr are growing throughout the tagging season).

The other independent variables used in the analysis include the PDSI (NOAA 2002), length of parr at tagging, and chinook redd counts in the eight streams (Fig. 3). The PDSI (Fig. 3*a*) is calculated by State Climate Division (NOAA 2002) and uses temperature and rainfall information in a formula to determine dryness. It uses a 0 as normal (mean), and drought is indicated by negative numbers, for example, –2 is moderate drought, –4 is severe drought, and –6 is extreme drought. PDSI varies among sites because they are in three different climate regions. Note that 2001 was an extreme drought year, whereas 1995 was extremely wet. The average length at tagging was calculated from PIT tagging records (PSMFC 2002). The average length at tagging (mm) for each site and year varies from a minimum of about 62 mm to a maximum of almost 95 mm (Fig. 3*b*). Redd survey

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Fig. 2. (*a*) The total number of chinook (*Oncorhynchus tshawytscha*) parr tagged from 1992 to 2001 (solid line) and the number of sites where tagging occurred (broken line); (*b*) means, minima, and maxima of the proportion of the survivors detected at Lower Granite Dam (LGR) for all sites in each year; and (*c*) means, minima, and maxima for the natural log of the estimated survival rates. Means are denoted by "–" and minima and maxima are denoted by the extent of the vertical lines.

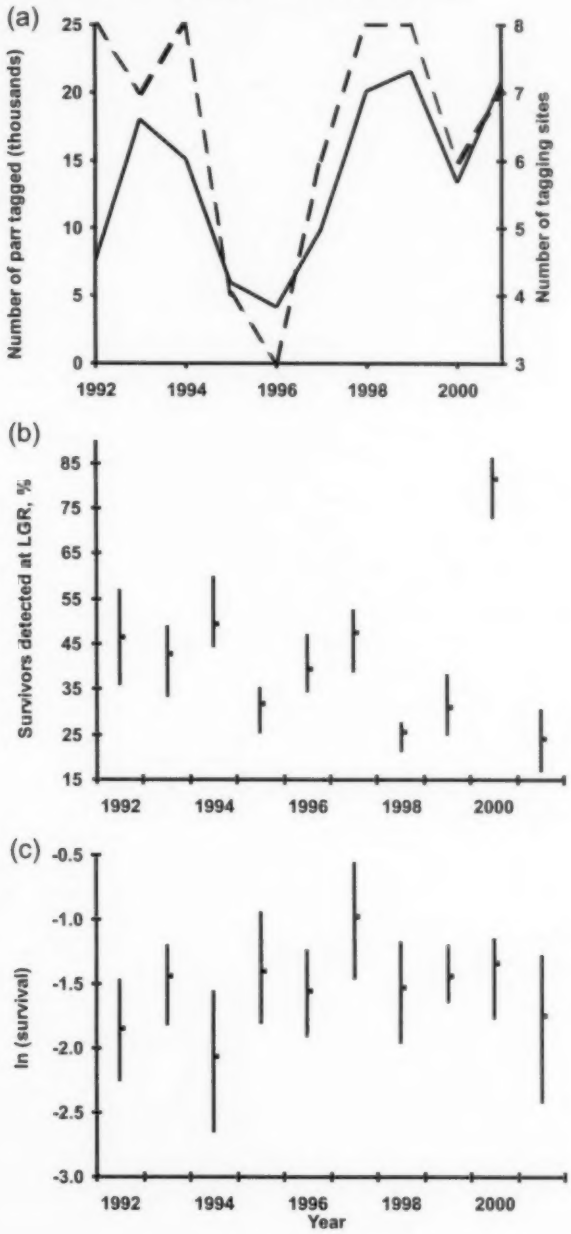
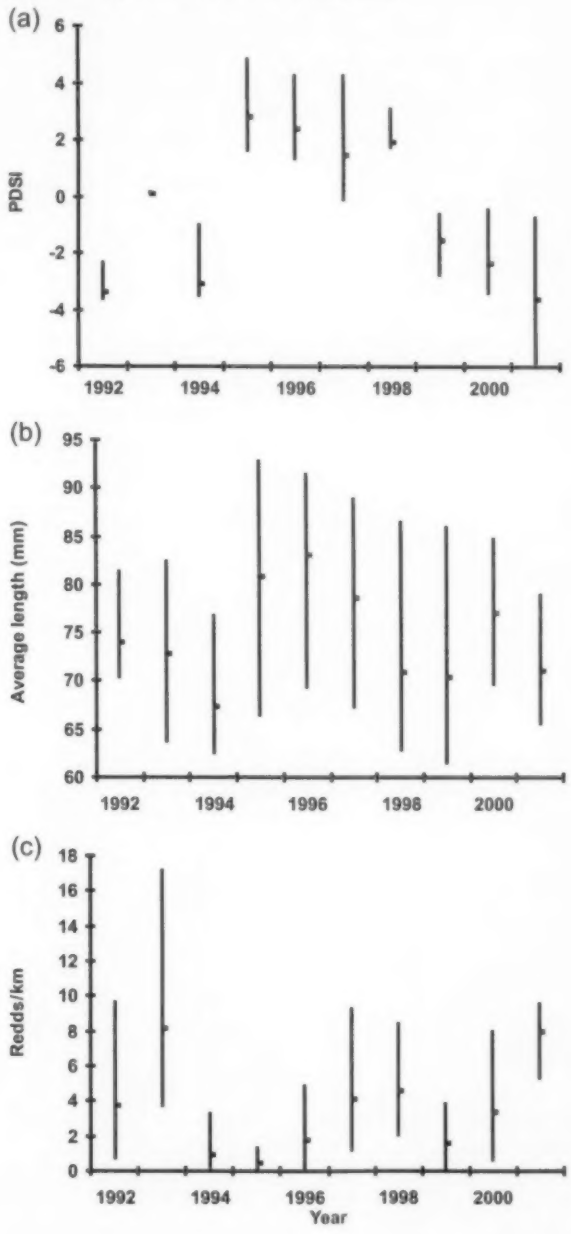


Fig. 3. (*a*) Means, minima, and maxima of the Palmer drought severity index (PDSI) for each climate region from July–December in the year of tagging; (*b*) means, minima, and maxima of the average parr length at tagging (mm) for each site and year; and (*c*) means, minima, and maxima of the redd density (redds/km surveyed) in the year of tagging at each site and in each year. Means are denoted by "–" and minima and maxima are denoted by the extent of the vertical lines.



information (redds counted and kilometres surveyed) was obtained from various sources for the spawning streams (P. Keniry, ODFW, 107 20th Street, LaGrande, OR 97850, personal communication (Grande Ronde River and Imnaha River basins), and Hassemer (1993); Elms-Cockrum 2001, updated by S. Keifer, IDFG, 600 S Walnut St., Boise, ID

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83707, personal communication (Salmon River basin)). Redd density in the year of tagging for each site varies from about 0.2 to 18 redds/km (Fig. 3*c*).

As noted, we had found in previous work that the PDSI and length at tagging were important correlates of survival (Paulsen and Fisher 2001). We included the redd density in the brood year (i.e., the year before tagging) and in the year of tagging for two reasons. First, we suspected that brood-year redd density might reveal a density-dependent relationship with survival: years of high redd density (and, by assumption, high parr density the following year) might have lower than average survival (e.g., Paulsen and Hinrichsen 2002). We further suspected that high redd densities in the year of tagging might be positively related to survival, based on a weak relationship noted in earlier work (Paulsen and Hinrichsen 2002). Year of tagging was included as a class or dummy variable in some models.

Methods

Conducting the power analyses requires the following elements: (1) retrospective or base-case estimates of survival rates and independent variables (see Data section); (2) retrospective models to summarize base-case survival rates; (3) methods to select among retrospective models that balance residual error with the number of estimated parameters; (4) prospective models, paralleling the retrospective models, and attendant assumptions to predict future survival rates, with and without habitat actions; (5) hypothesized effect sizes (changes in survival rates) associated with habitat actions; (6) an experimental design to assign treatment and control sites; and (7) statistical models for testing hypotheses about the effect size. These elements and their uses are described in detail below.

The general retrospective or base-case statistical log-linear model to summarize the past data is

$$(1)\qquad \ln(\hat{s}_{i,t}) = b_0 + R_i + Y_t + \gamma L_{i,t} + \delta D_{i,t} + \lambda D_{i,t-1} + \nu C_{i,t} + \varepsilon_{i,t}$$

where i indexes tagging site and t denotes year of tagging. $\mathrm{Ln}(\hat{s}_{i,t})$ is the natural log of survival to LGR, R_i are factor or classification variables (dummy variables for region or site), Y_t are year-specific classification variables common to all sites, $L_{i,t}$ is the average length of each group of parr at tagging (mm), $D_{i,t}$ are redd densities (redds/km) in year of tagging, $D_{i,t-1}$ are redd densities in the previous (brood) year, and the $C_{i,t}$ is the climate index (PDSI). The error terms ($\varepsilon_{i,t}$), a combination of process and measurement error, are assumed to be independently and normally distributed (0, σ^2). The terms b_0 (for the intercept), R_i, Y_t, γ, δ, and ν are estimated parameters. The "^" or hat term on the survivals is retained to emphasize the fact that they are estimated with measurement error. We applied a variety of common diagnostic techniques to the models used in the power analysis (see Results).

As noted in the previous section, we selected the independent variables based on recently published analyses for the chinook stocks in question. However, it is unclear if all variables should be included, and there are many possible forms for the models: all possible combinations of terms (e.g., (climate region or site or no R terms) × (year effects in or out) × (length at tagging in or out), etc.) yield 96 possible estimable models, ignoring potential interactions among variables. This is especially problematic because we have only 65 observations (site × year combinations) in the data.

Although stepwise regression is often used in similar circumstances, we instead used a recently developed information-theoretic approach (Burnham and Anderson 1998) to address this issue. We did so both because the approach gives a formal accounting for the relative plausibility of the models estimated and because we wanted to know to what degree more plausible retrospective regression models would result in higher power to detect the survival effects of habitat actions. Thompson and Lee (2002) have applied similar information-theoretic approaches to Snake River chinook spawner–recruit models.

A complete explanation of the information-theoretic approach described at length in Burnham and Anderson (1998) is beyond the scope of this paper. Briefly, however, the method consists of the following steps. (1) Identify a candidate set of models a priori, using information on scientifically plausible relationships between candidate independent variables and the dependent variable of interest. (2) Estimate the regression models using the same data set (the 65 observations described above, in this case). (3) For each model, calculate the Akaike information criterion (AIC), corrected for the number of estimated parameters. (4) Among the candidate models, select the model with the lowest AIC. Subtract the lowest AIC from each of the candidate models, yielding a "delta" which will be zero by definition for the model with the lowest AIC. (5) Calculate AIC weights for each model, using a simple exponential function of the deltas.

The weights are normalized to sum to one, and their values may be interpreted as the relative probability of each model, given the data and the set of candidate models. Note that the models may be non-nested, as is the case here, without affecting the comparisons. We estimated 10 candidate models; these include two models with either climate region or tagging site and all of the other independent variables shown in eq. 1 (models 1 and 2) and eight additional models, which we believed to be appropriate, based on past work. For the power analysis, we chose the most plausible and the least plausible models from the set of 10. Although we have used weights to account for measurement (sampling) error in earlier work (Paulsen and Fisher 2001), we did not do so in this case both for expositional simplicity and because they make very little difference in the results (Paulsen and Fisher, unpublished data).

Having summarized the historic data with simple log-linear regression models, we then simulated future "data". To do so, we first accounted for the variability or sampling error in the base-case survival estimates. We then accounted for variance in the parameter estimates and prediction error and finally projected future survival rates for the treatment and control sites, where the predictions incorporate both process and measurement error.

To account for sampling error (variability inherent in the 65 point estimates of survival), we generated nonparametric bootstrap estimates (Efron and Tibshirani 1993) of survival from the 141 000 release and detection records (one for each tagged fish). We used a nonparametric approach because sample size for some sites and years was quite limited (e.g.,

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only 43 parr were tagged in Johnson Creek in 1993) and we thought that normality assumptions for these cases might not hold in practice. This and all subsequent steps were done 10 000 times, each of which is referred to as a "replicate". The results from this step may be thought of as 10 000 possible historical "pasts", which should be a thorough sampling of past variation in the survival rate estimates. Simulated distributions of ln(survival) for Johnson Creek in 1993 and 2001 are displayed in Fig. 4. Note that although the means for the two years are nearly the same, the distribution is much broader for 1993, when fewer fish (43 vs. 6717) were tagged. Bootstrapping from the original records preserves these differences in the variance of the survival estimates. Bootstrapping is done by drawing from the original release-detection records and re-estimating maximum likelihood probabilities of survival for each site–year combination. The result for each replicate is a set of 65 maximum likelihood point estimates of survival (one for each site–year combination in the original data), but the point estimates will vary among replicates as a result of measurement error. In addition, because length at tagging was recorded for all fish, the bootstrapping also produced a distribution in fish size, an important covariate in the models.

Next, we estimated models identical to eq. 1 but using the simulated (bootstrapped) survival values just described:

$$(2)\qquad \ln(s^*_{i,t}) = b^*_0 + R^*_i + Y^*_t + \gamma^* L^*_{i,t} + \delta^* D^*_{i,t} + \lambda^* D^*_{i,t-1} + \nu^* C^*_{i,t} + \varepsilon^*_{i,t}$$

where the * denotes simulated values as just described, and the error terms are again assumed normally distributed (0, σ^{*2}). As with eq. 1, the error terms are a combination of process and measurement error. Note that the ^ has been omitted from the s^* term in eq. 2. With the exception of fish length (see above), values for the independent variables were assumed to be the same as in the past, real data series. Again, for each replicate, we estimate a model using eq. 2 above. By doing this for each of the 10 000 replicates, we obtained an approximation of the variability in the parameters owing to measurement error in the dependent variable and the variability in the process error.

Next, future simulated years are chosen at random from the 10 years of past data. The simulated values of future survival rates are then "predicted" using eq. 2 for each of the replicates:

$$(3)\qquad \ln(s^j_{i,t}{}^*) = b^j_0 + R^j_i + Y^j_t + \gamma^j L^j_{i,t} + \delta^j D^j_{i,t} + \lambda^j D^j_{i,t-1} + \nu^j C^j_{i,t} + E^j_{i,t} + \varepsilon^j_{i,t}$$

where j denotes replicate. That is, the $\ln(s^j_{i,t})$ terms in eq. 3 are predicted values based on the parameter estimates in eq. 2; the treatment effects, $E^j_{i,t}$; and the error term, $\varepsilon^j_{i,t}$, assumed to be normally distributed, are estimated with mean zero and variance σ^{*2} from eq. 2. The σ^{*2} estimated for each replicate (eq. 2) is used to preserve unexplained variability (both process and measurement error) in the predicted, future values of survival. The independent variable values, including year effects, were assumed to be the same as in the years randomly chosen from the simulated past "data" for each replicate, with the exception of length at tagging, as discussed above. Year effects (the Y^j_t terms) are estimated separately for future simulated years (2002, 2003, etc.), making them distinct from past year effects (1992–2001), to simulate what would happen in practice if an analyst had years of real posttreatment data in hand.

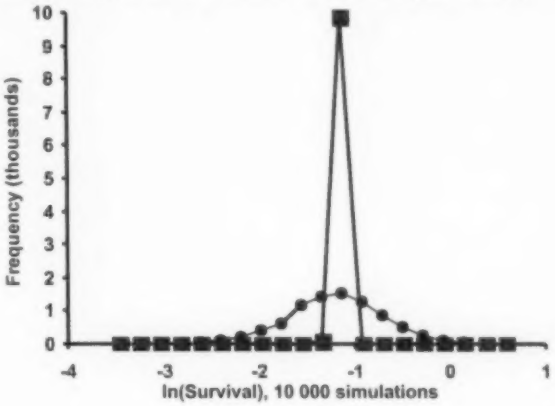

Fig. 4. Frequency distributions of simulated ln(survival) for Johnson Creek, 1993 (circles) and 2001 (squares). Forty-three parr were tagged in 1993, whereas 6717 were tagged in 2001.

Treatment effects, the $E^j_{i,t}$ terms (assumed to be the same over time for treatment sites once the habitat action is undertaken), are applied in eq. 3, with the effects being zero for all sites during pretreatment years (through 2001) and for control sites from 2002 onward. Treatment sites are assigned at random from the three sites not in wilderness areas (Table 1), with the other 5–7 sites being untreated controls. If, for example, treatment causes simulated survival to increase by 30% at treatment sites, then $E^j_{i,t}$ takes a value of ln(1.3) for treatment sites from 2002 onward, and zero otherwise. The dependent variable $\ln(s^j_{i,t}{}^*)$ in eq. 3 is, of course, increased by ln(1.3) (in the example) for treatment sites and unchanged for controls. The 10 000 replicates, drawn from the 141 000 tagging records, are used to account for measurement error in the dependent variable, with both process and measurement error (unexplained variation) accounted for using σ^{*2}.

The model in eq. 3 is similar to a BACI design (sensu Osenberg and Schmitt 1996). The "before" is the data simulated in eq. 2, whereas the "after" portion is the simulated future years from eq. 3, with the addition of treatment effects. We used both control sites and treatment sites, as described above, for the years 2002 onward. For each of the j replicates, we simply estimated a model as shown in eq. 3. The statistical power of the model is the proportion of the 10 000 replicates where the treatment effect, $E^j_{i,t}$, is estimated to be not equal to zero at $\alpha = 5\%$, using a two-tailed t test. As a check on the methods, we also examined the likelihood of rejecting a null hypothesis of no change when the simulated value of $E^j_{i,t}$ was in fact zero.

We employed a two-tailed test because some past habitat enhancement projects have resulted in deleterious effects on stream habitat and, presumably, juvenile chinook survival. For example, engineered habitat structures (i.e., gabions, wing walls, anchored logs) and inappropriate structures (i.e., those

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Table 2. Pearson's correlation coefficients for the natural log of survival, ln(*S*), and the continuous independent variables (PDSI = Palmer drought severity index).

	ln(*S*)	Length	Brood-year redd density	Tag-year redd density	PDSI
ln(*S*)	1.00	0.63*	–0.54*	–0.02	0.51*
Length		1.00	–0.48*	–0.15	0.39*
Brood-year redd density			1.00	0.13	–0.32*
Tag-year redd density				1.00	–0.08
PDSI					1.00

Note: An asterisk (*) denotes a significant correlation at $\alpha = 0.05$.

Table 3. Independent variables included in regression models for 10 candidate models for power analysis.

	Variables included						
Model	Region	Site	Year effects	Length	Tag-year density	Brood-year density	PDSI
1	X		**X**	**X**	X	**X**	X
2		**X**	**X**	**X**	X	**X**	X
3	X		**X**	**X**		**X**	
4		**X**	**X**	**X**		**X**	
5	X		**X**				
6		**X**	**X**				
7	X			**X**	X	**X**	**X**
8		X		**X**	X	**X**	**X**
9	X			**X**		**X**	**X**
10		X		**X**		**X**	**X**

Note: Region, site, and the year effects are classification or dummy variables (PDSI = Palmer drought severity index). Models 3 and 5, in bold type, are the best and worst models according to AIC (Akaike information criterion). Boldface **X** denotes significance at 5% or less.

that constrain an unconstrained stream reach) were often found to have severed linkages between the aquatic and riparian ecosystems (Kauffman et al. 1993). Beschta et al. (1991) found that engineered structures often broke down and left construction materials embedded in stream cobble which they believed would be detrimental to spawning adult and rearing juvenile salmonids. Furthermore, when these structures are inappropriately constructed for local conditions or fail, they often cause excessive erosion downstream and can present passage barriers to adult and juvenile salmonids (R. Vacirca, Ochoco National Forest Paulina District Office, 7803 Beaver Creek Road, Paulina, OR 97751, personal communication).

Results

The natural log of survival is positively correlated with length at tagging and the PDSI and negatively correlated with brood-year redd density (Table 2). Survival is very weakly correlated with tagging-year redd density, suggesting that this variable is unlikely to be important in the regression models.

We show the independent variables used in each of the 10 regression models (Table 3), with bolded Xs denoting significance at $\alpha = 5\%$ or less (two-tailed *t* test). Model 1 contains the regional classification variables and all of the independent variables except site (as they would be completely confounded). Model 2 is similar to model 1 but uses tagging sites as classification variables. The other eight models are all subsets of models 1 or 2. All 10 models are special cases of eq. 1, with some parameters constrained to equal zero.

We show the number of parameters and goodness-of-fit measures for the 10 models (Table 4). The number of parameters varies from 7 to 22. The AIC, delta, and $w(i)$ for each model also vary widely, as does the adjusted R^2. Note that the overwhelming majority of the $w(i)$ weight or plausibility is given to model 3 (0.963). The next highest model (model 1) has a weight of 0.035. Therefore, model 3 is clearly the most plausible of the set and has the third-highest adjusted R^2 (0.72). Model 5 has both the lowest weight and the lowest adjusted R^2 (0.42).

We show the details of the parameter estimates for these two regression models (eq. 1), the best and worst based on the AIC weights (Tables 5 and 6). For model 3, survival was somewhat lower in the Northeast Oregon region than in the South Fork Salmon and was significantly higher from 1997 through 1999 than in 2001. The latter is not too surprising, because 2001 was an extreme drought year (Fig. 3*a*). Length at tagging is positively related to survival, which again is no surprise; bigger fish are more likely to survive to LGR. Brood-year redd density has a negative relationship with survival, suggesting that a density-dependent relationship is present in the data. The results for the worst model, similar to model 3, but omitting length at tagging and brood-year redd density, are not very different from those for the most plausible model (Table 6). Although the year effects are broadly similar, with 1997 through 2000 associated with higher survival than 2001, survival in Northeast Oregon was higher

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Table 4. Model goodness of fit measures for 10 candidate models.

Model	No. of parameters	AIC	Delta	$w(i)$	$w(i)$ rank	Adjusted R^2
1	17	18.9	6.6	0.035	2	0.71
2	22	31.7	19.4	<0.001	4	0.72
3	15	12.3	0.0	0.963	1	0.72
4	20	25	12.7	0.002	3	0.72
5	13	53.7	41.4	<0.001	10	0.42
6	18	42.9	30.6	<0.001	8	0.59
7	8	34.9	22.6	<0.001	6	0.5
8	13	44.5	32.2	<0.001	9	0.5
9	7	33.1	20.8	<0.001	5	0.5
10	12	42.3	30.0	<0.001	7	0.5

Note: See text for definitions of Akaike information criterion (AIC), delta, and $w(i)$. Adjusted R^2 contains an adjustment for the degrees of freedom. Model numbers in bold type are the best and worst models according to AIC.

Table 5. Detailed regression results for model 3, which had the best Akaike information criterion.

Parameter	Value	Parameter estimate	Standard error	t ratio	Probability of >|t|
Intercept		–3.67	0.361	10.17	<0.0001
Region	Middle Fork Salmon River	–0.12	0.086	1.43	0.1538
	Northeast Oregon	–0.21	0.093	2.27	0.0233
	South Fork Salmon River	0.00	0.000	NA	NA
Year of tagging	1992	–0.22	0.114	1.91	0.0561
	1993	0.26	0.117	2.26	0.0239
	1994	–0.02	0.129	0.16	0.8751
	1995	–0.04	0.146	0.27	0.7854
	1996	–0.27	0.164	1.63	0.1039
	1997	0.47	0.127	3.70	0.0002
	1998	0.25	0.113	2.17	0.0297
	1999	0.37	0.114	3.22	0.0013
	2000	0.15	0.126	1.20	0.2319
	2001	0.00	0.000	NA	NA
Length at tagging		0.03	0.005	6.44	<0.0001
Brood-year density		–0.03	0.008	3.11	0.0020

Note: NA, not available.

Table 6. Detailed regression results for model 5, which had the worst Akaike information criterion.

Parameter	Value	Parameter estimate	Standard error	t ratio	Probability of >|t|
Intercept		–1.85	0.13	13.90	<0.0001
Region	Middle Fork Salmon River	0.12	0.10	1.28	0.2009
	Northeast Oregon	0.21	0.10	2.04	0.0416
	South Fork Salmon River	0.00	0.00	NA	NA
Year of tagging	1992	–0.11	0.16	0.69	0.4876
	1993	0.30	0.17	1.79	0.0738
	1994	–0.32	0.16	2.02	0.0437
	1995	0.32	0.20	1.63	0.1026
	1996	0.17	0.22	0.77	0.4442
	1997	0.74	0.17	4.30	<0.0001
	1998	0.22	0.16	1.36	0.1752
	1999	0.31	0.16	1.89	0.0582
	2000	0.41	0.17	2.35	0.0189
	2001	0.00	0.00	NA	NA

Note: NA, not available.

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Table 7. Power analysis results (proportion of replicates with significant estimate of treatment effects at $\alpha = 0.05$) for model 3.

Multiplicative survival increase	Years after treatment	One treatment site	Two treatment sites	Three treatment sites
0.3	1	0.15	0.20	0.23
	3	0.32	0.48	0.54
	5	0.46	0.67	0.74
	7	0.58	**0.80**	**0.86**
	9	0.69	**0.87**	**0.92**
0.5	1	0.31	0.42	0.49
	3	0.63	**0.83**	**0.89**
	5	**0.82**	**0.96**	**0.98**
	7	**0.92**	**0.99**	**1.00**
	9	**0.96**	**1.00**	**1.00**
0.7	1	0.48	0.63	0.69
	3	**0.83**	**0.97**	**0.98**
	5	**0.95**	**1.00**	**1.00**
	7	**0.99**	**1.00**	**1.00**
	9	**1.00**	**1.00**	**1.00**
0.9	1	0.64	0.78	**0.83**
	3	**0.93**	**0.99**	**1.00**
	5	**0.99**	**1.00**	**1.00**
	7	**1.00**	**1.00**	**1.00**
	9	**1.00**	**1.00**	**1.00**
1.1	1	0.76	**0.87**	**0.91**
	3	**0.97**	**1.00**	**1.00**
	5	**1.00**	**1.00**	**1.00**
	7	**1.00**	**1.00**	**1.00**
	9	**1.00**	**1.00**	**1.00**

Note: Bold numbers denote a power greater than 0.8.

Table 8. Power analysis results (proportion of replicates with significant estimate of treatment effects at $\alpha = 0.05$) for model 5.

Multiplicative survival increase	Years after treatment	One treatment site	Two treatment sites	Three treatment sites
0.5	1	0.20	0.26	0.30
	3	0.40	0.60	0.67
	5	0.58	**0.80**	**0.86**
	7	0.71	**0.90**	**0.94**
	9	**0.81**	**0.95**	**0.97**
0.7	1	0.30	0.41	0.48
	3	0.62	**0.82**	**0.89**
	5	**0.81**	**0.96**	**0.98**
	7	**0.91**	**0.99**	**0.99**
	9	**0.95**	**1.00**	**1.00**
0.9	1	0.41	0.55	0.62
	3	0.77	**0.94**	**0.97**
	5	**0.92**	**0.99**	**1.00**
	7	**0.98**	**1.00**	**1.00**
	9	**0.99**	**1.00**	**1.00**
1.1	1	0.52	0.67	0.74
	3	**0.87**	**0.98**	**0.99**
	5	**0.97**	**1.00**	**1.00**
	7	**0.99**	**1.00**	**1.00**
	9	**1.00**	**1.00**	**1.00**

Note: Bold numbers denote a power of greater than 0.8.

than the South Fork Salmon for this model. This suggests that the effects of brood-year redd density and length at tagging may be somewhat confounded with the classification variables.

We performed several diagnostic tests on the best and worst models. Although some autocorrelation is present in the independent variables, it was very weak and so was not incorporated into the power analyses. Studentized residuals and Cooke's D values (Belsley et al. 1980) revealed no serious problems with outliers or influential observations. As an additional test, we eliminated one tagging site or one tagging year of data at a time and re-estimated each model. The estimated parameters did not change by more than one standard deviation in the models using the resulting subsets of data. Finally, the residuals for both models appear to be normally distributed, passing common heuristic tests for normality (e.g., normality plots, Kolmogorov–Smirnov D).

We show the power analysis results for the best and worst models, respectively (Tables 7 and 8), using eq. 3 and subsets of the independent variables in models 3 and 5. For convenience, we only show results for the odd years of simulated experiments, although the models were run for 10 years. As one might expect, a null hypothesis of no effect was rejected approximately 5% of the time when the actual effect size was, in fact, zero (results not displayed in tables). For the most plausible model (Table 7), a 30% increase in survival (i.e., survival in treatment streams is 1.3 times base-case survival) can be detected with power of 0.8 with two treatment sites, five control sites, and 7 years of posttreatment data. For increases less than 30% (not shown here), power was always less than 0.8. With three treatment sites and 7 years of posttreatment data, power for the 30% improvement increases to 0.86. A power of at least 0.8 can be attained within 1 to 3 years by using two to three treatment sites, at survival increases of 90% and 110% (chosen to bracket the doubling in survival used by Paulsen and Hinrichsen (2002)). Power is essentially 1.0 within 3 years.

Power is obviously lower for the worst model (Table 8), although the difference is not large. Power is always less than 0.8 for the 30% increase in survival, and power is somewhat lower than the best model for the higher increases in survival. On the other hand, the 90% and 110% increases in survival are detectable with high power within 3 years, even when using only one treatment site.

Discussion

The approach that we have employed is somewhat unusual in that it combines information-theoretic methods (Burnham and Anderson 1998) for model selection with conventional hypothesis testing that underlies the power analysis itself. At least in this example, the most plausible and least plausible models yielded similar results for the power analysis, despite having very different goodness-of-fit, whether measured using AIC or adjusted R^2. Although the least plausible model had lower power, especially when increases in survival were small, the difference between the two models was not as large as we had expected.

The focus of this paper is on power analysis methods, but an important practical question is how useful the data and techniques may be in practice, given the regulatory require-

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ments noted in the introduction. On one hand, the use of parr-to-smolt survival data has the potential to increase power to detect juvenile survival increases substantially, when compared with using recruits per spawner estimates for the same purpose. This suggests that if such increases are feasible and can occur fairly quickly following habitat actions, then experiments need only be run for a few years to detect parr-to-smolt survival changes.

On the other hand, it is somewhat discouraging that the minimum reliably detectable increase in survival is 30%, especially because increases of this magnitude have rarely been documented in actual field studies. One possible exception is Solazzi et al. (2000) for coho salmon. They estimated a threefold increase in coho survival (pretreatment mean of 13% to posttreatment mean of 38%). However, they used abundance estimates at the parr and smolt stages, rather than tagging studies, to estimate survival (i.e., number of smolts/number of parr = survival rate). They do not present data on the precision of their annual survival estimates, but we suspect that the precision may not be very high. Whether or not their results for coastal coho would generalize to inland chinook is another unknown at this point.

In addition, it is not clear what proportion of the parr at any give site will actually benefit from habitat modifications, because juvenile chinook tend to be highly mobile. For example, Bjornn (1978) concluded that substantial numbers of chinook fry (which are too small to be PIT tagged) left their rearing areas in the Lemhi River, a tributary to the Salmon River, shortly after emerging from the redds. These early outmigrants might well be unaffected by survival increases from habitat actions that only influence juveniles with longer residence times in rearing areas in which habitat actions often occur. Some actions, such as decreasing fine sediment in spawning gravel, aim to increase egg-to-fry survival. These and other actions are unlikely to significantly influence parr-to-smolt survival, so the parr-to-smolt data would be of little use. In addition, because fry (let alone eggs) are probably too small for unique marks (such as PIT tags), evaluating changes in very early life stage survival rates will be a technically challenging task.

In light of these problems, we suggest three potential directions for future research. The most important of these, of course, is to begin conducting actual fieldwork. Although the power analysis described here provides some guidance on detecting effects (if the assumptions of the models hold in practice), it is no substitute for the results of real-world experiments. A second possibility would be to use parr-to-smolt survival estimates for sites in the Snake River where substantial habitat work has been carried out over the past decade or so (e.g., the Clearwater and Upper Salmon subbasins) in combination with untreated controls (e.g., Sulphur Creek and other areas that have received few if any treatments) to see if the effects of past actions on parr-to-smolt survival are apparent in existing data. This approach is less than ideal, as the tagging programs were not designed to detect such effects, but it may provide some additional guidance on designing future experiments.

Finally, we suspect that it would be useful to investigate combining parr-to-smolt survival and recruit per spawner estimates into a single analytical model. The purpose would be to discover to what degree differences in parr-to-smolt survival explain differences in recruits per spawner among stocks and provide reliable, early indicators of changes in recruits per spawner over time. At present, the temporal overlap between the two data series is very limited — the latest available recruits per spawner estimates end with brood year 1996, because one must wait 5 years for all adults to return from a given spring–summer chinook brood before calculating recruitment to adulthood. This is only 4 years after the 1992 start of the parr-to-smolt survival estimates. A preliminary analysis (Paulsen, unpublished data) suggests that the parr-to-smolt survival estimates add little explanatory power to spawner–recruit models. However, whether this occurs because of limited data or is caused by other problems (e.g., many fry leaving rearing areas before they can be tagged) is unknown at present.

In summary, the power analysis provides guidance for design of future experiments, but it cannot substitute for field research. That is, by itself it cannot answer the question posed by NMFS: do habitat actions increase salmonid survival? Instead, it answers a related but different question: if habitat actions do increase fish survival, how should experiments be designed to reliably detect the increase?

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A temperature- and size-dependent model of sand shrimp (*Crangon septemspinosa*) predation on juvenile winter flounder (*Pseudopleuronectes americanus*)

David L. Taylor and Jeremy S. Collie

Abstract: We investigated the temperature-mediated vulnerability of postsettled winter flounder (*Pseudopleuronectes americanus*) to sand shrimp (*Crangon septemspinosa*) predation. Small increases in flounder growth rates substantially decreased predator-induced mortality. Recent warming trends in Northwest Atlantic estuaries can increase flounder survival by accelerating growth and minimizing the duration during which juveniles are susceptible to size-dependent predation. Extreme temperature increases, however, depress growth because a disproportionate amount of energy is devoted to increased metabolism, leaving less for somatic development. Flounder survival is also reduced during warm years because of intensified shrimp predation. Moreover, interannual variations in temperature affect the relative timing of shrimp migration and flounder settlement, thus controlling the spatial and temporal overlap between predator and prey. Predicted flounder abundance and survival were statistically unrelated to observed flounder abundance sampled annually during late spring. However, model predictions and field data suggest that flounder abundance is maximal in years when seasonally averaged temperature is approximately 16 °C. Above and below this temperature, flounder year-class size is considerably lower, possibly as a result of temperature effects on trophic dynamics. We conclude that shrimp predation is a significant source of mortality for postsettled flounder, but it is not the sole determinant of interannual variations in recruitment.

Résumé : Notre étude examine la vulnérabilité des plies rouges (*Pseudopleuronectes americanus*), après leur établissement sur le fond, à la prédation par la crevette grise des sables (*Crangon septemspinosa*), une vulnérabilité qui est reliée à la température. Un léger accroissement dans les taux de croissance des plies diminue de façon importante la mortalité due à la prédation. Les tendances récentes de réchauffement dans les estuaires du nord-ouest de l'Atlantique peuvent augmenter la survie des plies en accélérant la croissance et en minimisant la période pendant laquelle les jeunes plies sont vulnérables à cette prédation reliée à la taille. Cependant, des accroissements extrêmes de température ralentissent la croissance, car une quantité excessive de l'énergie est consacrée à l'augmentation du métabolisme, au détriment du développement somatique. La survie de la plie est aussi réduite les années plus chaudes à cause d'une intensification de la prédation par les crevettes. De plus, les variations thermiques d'une année à l'autre affectent les moments relatifs de la migration des crevettes et de l'établissement des plies; elles contrôlent donc les chevauchements temporels et spatiaux du prédateur et de la proie. L'abondance et la survie prédites chez la plie sont statistiquement indépendantes de l'abondance des plies dans les échantillons annuels prélevés à la fin du printemps. Cependant, les prédictions du modèle et les données de terrain indiquent que l'abondance des plies est maximale les années où la température moyenne calculée sur toute la saison est de l'ordre de 16 °C. En deçà ou au-delà de cette température, la classe d'âge des plies de l'année est fortement réduite, probablement à cause des effets de la température sur la trophodynamique. En conclusion, il apparaît que la prédation par les crevettes est un facteur important de mortalité chez les plies après leur établissement, mais que ce n'est pas la seule cause des variations inter-annuelles du recrutement.

[Traduit par la Rédaction]

Introduction

A primary objective of fisheries research is to understand the processes that regulate recruitment. Hjort (1914) hypothesized that year-class size is controlled during a critical period in the early life history of the fish. This original hypothesis has been refined as a series of ontogenetic bottlenecks in which the principal processes thought to control recruitment include fluctuations in oceanographic and climatic conditions, variations in food availability, predation, and resource com-

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petition (Anderson 1988; Bailey and Houde 1989). As these mechanisms operate simultaneously and potentially interact with one another, a thorough analysis of the factors controlling year-class size is very difficult.

Despite the complications inherent to exploring the timing and nature of mortality factors in many fish species, flatfish have received considerable attention in this area of research (Bailey (1994) and references therein). Of particular interest, the winter flounder (*Pseudopleuronectes americanus*) is an ecologically and commercially important flatfish along the northeast coast of North America. The New England – mid-Atlantic winter flounder stock complex has been heavily exploited in the recent past, consequently decreasing stock abundance to very low levels (Northeast Fisheries Science Center (NEFSC) 2003). Under the advisement of the National Marine Fisheries Service and the Atlantic States Marine Fisheries Commission, management plans were enacted to reduce further stock losses owing to fishing mortality. The rebuilding process has been successful for most of the New England – mid-Atlantic stock complex, but subpopulations of winter flounder in several southern New England estuaries are not following this regional trend and attempts to rebuild these depleted stocks have been unsuccessful.

The decline in localized winter flounder populations coincides with a significant warming trend in many Northwest Atlantic estuaries (Keller and Klein-MacPhee 2000). Several investigators proposed that elevated water temperatures might intensify predator-induced mortality on the early life stages of flatfish by increasing the metabolism and subsequently the consumption rate of potential benthic predators (Van der Veer et al. 1990; Keller and Klein-MacPhee 2000). There is also evidence suggesting that processes affecting the survival of juvenile flatfish are critical determinants of year-class strength (Bailey 1994). Accordingly, the interactive effects of temperature on the predator-induced mortality of postsettled winter flounder warrant further investigation.

Winter flounder spawn demersal eggs inside estuaries in winter and early spring (Pearcy 1962). After hatching, the larvae are pelagic for about 60 days, after which the larvae metamorphose into juveniles and settle to the benthos (Pearcy 1962). The small size of recently settled winter flounder (ca. 8–9 mm total length (TL); Chambers and Leggett 1987) and their relatively weak swimming and burying capabilities make this species particularly vulnerable to crustacean and demersal fish predators (Manderson et al. 1999, 2000; Fairchild and Howell 2000). The result is intense predator-induced mortality and thus possible year-class determination at the postsettlement stage.

Predation by the sand shrimp (*Crangon septemspinosa*) has been implicated as one of the most significant sources of mortality for recently settled winter flounder (Witting and Able 1995). The relative magnitude of crangonid shrimp predation on flatfish is influenced by several factors, perhaps the most important being prey body size (Van der Veer et al. 1990; Gibson et al. 1995). A common inference is that the risk of death owing to predation (i.e., susceptibility) is reduced with increased fish size. Winter flounder are most susceptible to *C. septemspinosa* predation at settlement, when fish are small in size and completing several aspects of morphological and ecological metamorphosis (Witting and Able 1995). Susceptibility to predation then gradually decreases after settlement until a refuge is attained when flounder reach 24 mm TL (Witting and Able 1995). Thus, faster-growing flounder are likely to have a survival advantage because their exposure to the "mortality window", a period lasting several months characterized by high predator-induced mortality, is shortened.

What temperature conditions optimize postsettled winter flounder survival? The varying physiological and behavioral responses by *C. septemspinosa* and juvenile flounder to increased temperature can enhance or impede predation intensity. Increased water temperature could be detrimental to flounder survival if the primary effect were to accelerate shrimp metabolism and thus enhance the predator's foraging activity. Conversely, elevated temperatures are likely to increase flounder growth rates and thus minimize the duration during which juveniles are susceptible to size-dependent predation. Ancillary to these two counteracting processes, temperature also influences the relative timing of shrimp seasonal onshore migrations (Price 1962; Haefner 1969, 1979) and the metamorphosis and subsequent settlement of flounder to the benthos (Laurence 1975; Chambers and Leggett 1987), thus controlling the spatial and temporal overlap between predator and prey. It is the combination of these factors that must be considered to obtain a clear understanding of how temperature regulates *C. septemspinosa* predation on recently settled winter flounder.

Previous investigations focusing only on the monotonic relationships between growth and survivorship have not recognized the possible synergistic effects of temperature on the key elements of the predation process. The purpose of this study was to integrate temperature-mediated responses of *C. septemspinosa* and postsettled winter flounder that impact the vulnerability of fish to shrimp size-dependent predation. A deterministic model was developed to track the daily growth and mortality of a cohort of juvenile flounder as the fish progressed through a mortality window. To determine which temperature-mediated responses exerted the largest impact on juvenile flounder survival and mortality, various model simulations were run altering initial values of flounder growth rates, water temperature, and fish and shrimp settlement and migration patterns. Flounder survival predicted from the deterministic model was statistically compared with field observations of juvenile abundance from two Northwest Atlantic estuaries to determine if shrimp predation accounts for annual variations in flounder year-class strength.

Materials and methods

Model description and parameterization

The temperature- and size-dependent deterministic model estimated the cumulative and average daily instantaneous mortality (M and Z) of a single cohort of postsettled flounder as the fish progressed through a mortality window. The time scale of the mortality window was defined (unless explicitly stated otherwise; see Model simulations) from initial flounder settlement (31 March, body size = 8 mm TL) and concluded once fish achieved a body size large enough to preclude them as prey for shrimp (24 mm TL; Witting and Able 1995). The first assumption of the model was that the initial density of the cohort was 200 flounder·100 m^{-2}. The assumed initial value of flounder density is in good agree-

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ment with field estimates from sampling in several Northwest Atlantic estuaries (Sogard et al. 2001; Curran and Able 2002; Dominion Nuclear Connecticut (DNC) 2002). The second assumption of the model was that shrimp did not grow during the predation period (i.e., mortality window), and thus flounder mortality was evaluated without the confounding effects of changing predator size (Rice et al. 1993; Paradis et al. 1999). The third assumption was that flounder mortality was due entirely to predation by the shrimp *C. septemspinosa*. The information used to construct this model was generated from laboratory experiments and field data collected in Narragansett Bay, Rhode Island (R.I.), and Niantic River, Connecticut (Conn.). Thus, the simulated flounder cohort and its interaction with predatory shrimp modeled conditions typically found in northeastern estuaries of the United States.

Daily temperatures incorporated into model simulations were generated from a regression equation derived by Rose et al. (1996). The regression equation was fit to observed bottom water temperatures (n = 1380) recorded in Narragansett Bay (41°32.8′, 71°24.4′) from 1959 to 2000. The long-term average was determined by fitting a trigonometric function with an iterative least-squares procedure (Microsoft Excel Solver, Fylstra et al. 1998):

$$(1) \qquad T = 11.454 - 7.444\cos(0.0175\text{day}) - 6.626\sin(0.0175\text{day})$$

where "day" represents the day of the year and 0.0175 converts degrees to radians (Rose et al. 1996).

Daily growth rates of postsettled flounder were calculated from a temperature- and weight-specific bioenergetic model outlined in Rose et al. (1996):

$$(2) \qquad W_t = W_{t-1} + pC_{\max}\text{AE} - R_{\text{tot}}$$

where W_t is weight in milligrams incremented daily, $C_{\max}$ is the maximum consumption rate (mg·day^{-1}), p is the proportion of $C_{\max}$ realized (p = 0.766), AE is the assimilation efficiency (AE = 0.7; Ware 1975), and R_{tot} is the total metabolic rate (mg·day^{-1}).

Reported growth estimates of juvenile winter flounder in northwestern and mid-Atlantic estuaries range between 0.22 and 1.39 mm·day^{-1} (Buckley and Caldarone 1988; Meise et al. 1999; Sogard et al. 2001). In the current model, the proportion of $C_{\max}$ realized (p) was fixed at 0.766 to ensure that the average daily growth rate of flounder through the mortality window was equal to 0.50 mm·day^{-1}. This is a moderate growth rate according to reported values (Buckley and Caldarone 1988; Meise et al. 1999; Sogard et al. 2001) and hereafter is defined as a "mean" growth rate representing the baseline condition (see Model simulations). Maximum consumption ($C_{\max}$) and losses owing to metabolic activity (R_{tot}; mg·day^{-1}) depend on an individual's weight and water temperature. A complete description of $C_{\max}$ and R_{tot} parameterization is provided by Rose et al. (1996).

The mean weight (W_t; mg) calculated for flounder was converted into a daily increase in total length (TL_t; mm) based on the following length–weight relationship (Rose et al. 1996):

$$(3) \qquad \text{TL}_t = 10.723W_t^{0.28}$$

Mean daily growth and the resulting body size of flounder were incorporated into a size-, temperature-, and density-dependent predation mortality model. The number of surviving flounder at a given daily time step was calculated as

$$(4) \qquad N_t = N_{t-1} - N_e \times 100$$

where N_t is the number of flounder·100 m^{-2} surviving to time t, N_{t-1} is the number of flounder·100 m^{-2} at the previous daily time step, and N_e is the number of flounder consumed daily (number of flounder eaten·m^{-2}), multiplied by 100 to standardize mortality losses and subsequent abundance levels to the number of individuals·100 m^{-2}.

The number of flounder consumed at each daily time step (N_e) was modeled as the product of gross vulnerability, feeding period, and shrimp density:

$$(5) \qquad N_e = G_V F \rho_s$$

where G_V is gross vulnerability (number of flounder eaten·shrimp^{-1}·m^{-2}·h^{-1}), F is the feeding period of shrimp (h) during a daily time step, and ρ_s is the density of shrimp (number of shrimp·m^{-2}). The gross vulnerability of flounder to predation is the product of four events that constitute the "predation sequence". In an analysis of the behavioral mechanisms underlying *C. septemspinosa* size-dependent predation on winter flounder, Taylor (2003) quantified each component of the predation sequence as a function of flounder size (TL; mm), flounder density (ρ_f; number of flounder·m^{-2}), and water temperature (T; °C) (Table 1). The predation sequence was defined as the number of encounters (E) between shrimp and flounder (number of encounters·shrimp^{-1}·m^{-2}·h^{-1}), and the probability of flounder being attacked (P_A), captured (P_C), and ingested (P_I) by a shrimp given the previous event in the sequence (Table 1). Each component of the predation sequence was incorporated into the current model (i.e., $G_V = E\,P_A\,P_C\,P_I$) and was recalculated daily based on flounder size (eq. 3), flounder density (eq. 4; standardized to units of number of flounder·m^{-2}), and water temperature (eq. 1).

To calculate the total number of flounder consumed daily (N_e), the gross vulnerability of flounder (G_V) was multiplied by the feeding period of shrimp (F; h) during a daily time step and the density of shrimp (ρ_s). *Crangon septemspinosa* require 6–12 h after feeding to empty the cardiac portion of their stomach (Wilcox and Jeffries 1974). Moreover, crangonid shrimp generally exhibit two periods of peak foraging activity during the night with each event lasting approximately 2 h (Hagerman 1970; Wilcox and Jeffries 1974). The feeding period of shrimp (F) in model simulations was therefore fixed at 4 h over a complete daily cycle.

The density of shrimp (ρ_s) was determined from spring and summer field surveys conducted in shallow estuarine waters (<1.5 m) of Narragansett Bay in 2001 (D.L. Taylor, unpublished data). Only those shrimp greater than 40 mm TL were determined to be predators of winter flounder (D.L. Taylor, unpublished data) and their densities were calculated as

$$(6) \qquad \rho_s = -0.0007(\text{day}^2) + (0.2051\text{day}) - 13.259$$

The resulting densities predicted from the second-order polynomial increase at a decelerating rate during simulations and correspond well with previous reports of adult sand shrimp

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Table 1. Components of the predation sequence for the sand shrimp (*Crangon septemspinosa*) preying on juvenile winter flounder (*Pseudopleuronectes americanus*).

Predation sequence	Equation
Encounters	$E = -40.788 + 2.655\mathrm{TL} + 3.640\rho_f + 0.041T$
Attack probability	$\mathrm{Logit}(P_A) = -6.572 + 0.110\mathrm{TL} + 0.045\rho_f + 0.227T - 0.003\rho_f T$
Capture probability	$\mathrm{Logit}(P_C) = -1.407 + 0.003\mathrm{TL} - 0.013\rho_f - 0.023T$
Ingestion probability	$\mathrm{Logit}(P_I) = 6.923 - 0.527\mathrm{TL} + 0.009\rho_f + 0.053T$

Note: Components are estimated as a function of flounder total length (TL; mm), flounder density (ρ_f; number of flounder·m^{-2}), and water temperature (T; °C). Encounters (E) are units of number encounters·shrimp^{-1}·m^{-2}·h^{-1}. Attack, capture, and ingestion probabilities (P_A, P_C, and P_I, respectively) are the natural logarithm of the ratio of response frequencies (Logits). $\mathrm{Logit}(P) = \log[P/(1 - P)]$ (from Taylor (2003)).

abundance in northern-temperate estuaries (Price 1962; Modlin 1980).

Model simulations

Baseline model simulations were run according to the previously discussed equations and parameters (see Model description and parameterization). Subsequent simulations determined which temperature-mediated responses exerted the largest impact on flounder survival and mortality. For each model simulation, flounder daily growth (G; mm·day^{-1}), temperature (T; °C), and predator density (ρ_s; number of shrimp·m^{-2}) were averaged over the length of the mortality window (MW; number of days required to grow from 8 to 24 mm TL). Daily instantaneous mortality rates (Z) of flounder were also averaged over the number of days that fish were vulnerable to shrimp predation. Cumulative mortality rates (M) were estimated from initial flounder density (200 flounder·100 m^{-2}) at 31 March (day 90) and the number of flounder remaining at the end of the respective mortality window.

Several investigators have argued that relatively small variations in larval and juvenile fish growth rate, and thus size-at-age, can cause order-of-magnitude differences in the number of individuals surviving to the next life history stage (Bailey and Houde 1989; Pepin 1990; Rice et al. 1993). Simulation I analyzed the effect of flounder growth variation on fish survival when all individuals within the cohort were experiencing the same temperature conditions (within-year variability in flounder growth). Flounder growth rates were increased and decreased by 25% and 50% of the mean daily growth estimated from baseline simulations. An additional "growth" simulation was run using a broader and continuous range of flounder growth rates (G = 0.1–1.5 mm·day^{-1} measured at 0.01-mm increments) and the cumulative mortality (M) was calculated every 20 days after settlement (i.e., M at 20, 40, and 60 days after settlement).

Flounder cohorts experience different temperature regimes between years. Given that temperature has a potentially large effect on fish growth, flounder mortality rates are also likely to change with varying environmental conditions. Moreover, differences in annual spring water temperature are expected to impact shrimp predation intensity, thus affecting flounder survival (between-year variability in growth and predator behavior). Simulation II examined the effects of temperature on flounder growth and the components of the predation sequence (Table 1) by increasing and decreasing bottom water temperature by 2 and 4 °C daily (eq. 1). An additional simulation was run using a broader and continuous range of seasonally averaged temperatures (average daily T from day 90 to day 150 = 5.0–15.0 °C measured at 0.01 °C increments) and the cumulative mortality (M) was calculated every 20 days after settlement (i.e., M at 20, 40, and 60 days after settlement).

Simulations I and II assumed a constant flounder settlement date (day 90). Metamorphosis and subsequent settlement of developing flounder, however, are relatively variable, particularly with variations in interannual temperature (Laurence 1975; Sogard et al. 2001). The next series of model simulations considered the effect of different times of flounder settlement on mortality rates by increasing and decreasing settlement date (day of year) by 14 days. Simulation IIIA allowed bottom water temperature to vary according to eq. 1 (early settlers were exposed to colder temperatures than late settlers). In simulation IIIB, initial water temperature was held constant regardless of the settlement date (early settlers were exposed to the same temperatures as late settlers).

The density of sand shrimp predators has considerable implications for juvenile winter flounder survival (Witting and Able 1995). Simulations thus far have assumed that shrimp density varied in time according to eq. 6. However, like flounder settlement, crangonid shrimp onshore migrations exhibit interannual variation, controlled primarily by the increase in spring water temperature (Price 1962; Boddeke 1976; Haefner 1979). The final model simulation determined the effect of shrimp migration, and consequently temporal trends in shrimp density, on flounder mortality. In simulation IVA, shrimp density was either lagged or advanced by 14 days while maintaining a fixed flounder settlement date (day 90). Thus, situations when shrimp migration was premature (or delayed) resulted in flounder being exposed to a higher (or lower) density of predators. Simulation IVB allowed flounder settlement to vary at the same rate as shrimp migration (lagged or advanced by 14 days).

Field sampling and comparisons with model outputs

To estimate the abundance of juvenile winter flounder in the field, samples were collected at 18 stations throughout Narragansett Bay (J. Christopher Powell, R.I. Division of Fish and Wildlife, Fort Wetherill Marine Laboratory, 3 Fort Wetherill Road, Jamestown, RI 02835, personal communication). One seine haul covering 500 m^2 was conducted from a boat at each of the 18 stations with a 61 × 3.05 m beach-seine set (0.64-cm mesh size and 0.48-cm bunt). Field sampling was limited to shallow habitats that are inhabited by shrimp and juvenile flounder during late spring. Flounder catch and length–frequency data were collected in June from 1988 to 2001, at which time flounder had reached a size large enough that they were no longer vulnerable to shrimp,

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thus ensuring that all mortality caused by shrimp predation was accounted for. Estimated abundance of flounder caught in Narragansett Bay was standardized to number of individuals·100 m^{-2} and calculated assuming 30% efficiency of the sampling gear (Pierce et al. 1990).

The abundance and length–frequency of juvenile winter flounder in Niantic River was monitored at two shallow, nearshore stations from 1983 to 2001 from late May to June (DNC 2002). Biweekly sampling occurred with a 1-m beam trawl equipped with two tickler chains and nets of 0.8- and 1.6-mm mesh. Four tows were made per sampling date (two from each net of different mesh size) covering a distance of ~40 m. The number of flounder in each of the four replicate tows was averaged and standardized to number of individuals·100 m^{-2} and calculated assuming 60% efficiency of the sampling gear (Pierce et al. 1990).

Flounder survival predicted from the deterministic model was statistically compared with field observations of juvenile abundance to determine if shrimp predation accounts for annual variations in flounder year-class strength. The model was parameterized according to annual variations in temperature, initial cohort size, and the timing of flounder settlement and shrimp migration into estuarine habitats. Narragansett Bay water temperature was calculated from weekly samples collected at Fox Island (41°32.8′, 71°24.4′) from 1988 to 2001 (University of Rhode Island, Graduate School of Oceanography, Narragansett, R.I., URI/GSO Bottom Trawl Survey, unpublished data). Estimates of Niantic River water temperatures were obtained from continuous temperature recorders at the intakes of the Millstone Power Plant Station, Waterford, Conn. (DNC 2002). Daily temperatures were generated from separate regression equations (eq. 1) fit to observed water temperature for each year and area (Narragansett Bay or Niantic River).

For this part of the study, the deterministic model tracked the growth and survival of three cohorts of juvenile flounder as the fish progressed through the mortality window. The initial cohort sizes were scaled according to reported values of flounder larval abundance (number of larvae·100 m^{-3}) sampled for the same year-class (Narragansett Bay: PG&E Generating and Marine Research, Inc. (1999) and Michael D. Scherer, Marine Research Inc., 141 Falmouth Heights Road, Falmouth, MA 02540, personal communication; Niantic River: DNC 2002). The size of the three cohorts for a given year was determined by multiplying the mean size of a cohort (200 flounder·100 m^{-2}·$cohort^{-1}$) by the proportion of mean larval abundance for the same year-class. For example, larval abundance in 1983 (Niantic River) was 50% (23.3 larvae·100 m^{-3}) of the mean larval abundance estimated from 1983 to 2001 (46.2 larvae·100 m^{-3}) (Table 2). Thus, the initial settling density for the three individual cohorts in Niantic River in 1983 was 100 flounder·100 m^{-2}·$cohort^{-1}$ (300 total flounder·100 m^{-2}).

The timing of flounder settlement for a given year was determined from the size distribution of juveniles measured during field sampling in late spring and back-calculating growth to the day of the year that flounder were 8 mm TL (i.e., size at settlement). Flounder size was back-calculated according to the temperature- and weight-specific growth model presented earlier (eqs. 2–3). The three individual cohorts settled at different times of the year according to the variance in size distribution observed during field sampling in late spring. The settling date for the second of three flounder cohorts was determined by back-calculating growth from the mean total length of flounder measured during field sampling. The settling date of the first and third cohorts was determined by back-calculating growth from a starting size equal to ± standard deviation of mean body size. For example, the size of flounder in Narragansett Bay in 1988 (sampling day = 189) was 55.7 ± 10.4 mm TL (Table 2). Back-calculating each size (45.3, 55.7, and 66.1 mm TL) to the day of the year when flounder were 8 mm TL resulted in settling dates of 101, 115, and 126 for cohorts 1, 2, and 3, respectively.

Calculating shrimp densities as a function of temperature (as opposed to day of the year; eq. 6) allowed for interannual variations in shrimp migration patterns. In Narragansett Bay, for example, the annual arrival of shrimp into flounder settling grounds occurred at 5.8 °C, peak predator densities at 14.1 °C, and the migration of shrimp out of settling grounds when temperatures reached 20.5 °C.

A rank correlation coefficient (Kendall's τ) was used to test for the significance of association between the number of flounder predicted to survive beyond the mortality window and the observed flounder abundance sampled annually in Narragansett Bay (1988–2001) and Niantic River (1983–2001) during late May to June. Evidence of density-dependent mortality during the early juvenile period was also examined for both model and field data. Density dependence was tested by fitting a least-squares linear regression to flounder instantaneous mortality and the natural logarithm of flounder settling density (three cohorts combined; number of flounder·100 m^{-2}). Estimates of instantaneous mortality rates for model-predicted data were calculated as the difference in natural logarithm of abundance between initial flounder settling density (described above) and the predicted flounder abundance at the end of the mortality window. Estimates of instantaneous mortality rates for field data were calculated as the difference in natural logarithm of abundance between initial flounder settling density (described above) and the observed flounder abundance during field sampling in late May to June (Table 2).

Results

Growth and predation models

Postsettled flounder growth was size- and temperature-dependent (Fig. 1). Maximum growth for 8, 16, and 24 mm TL flounder was 0.60, 0.71, and 0.79 mm·day^{-1}, respectively, and occurred at 12.2 °C (Fig. 1). Model baseline conditions simulated growth according to eqs. 2–3 (Rose et al. 1996). The average mean growth for flounder developing through the mortality window was 0.50 mm·day^{-1}. During this period, flounder were exposed to an average daily temperature of 7.32 °C and were vulnerable to shrimp predation for 33 days (Table 3).

At a fixed density of 2 flounder·m^{-2} and flounder body size greater than 12 mm TL, the encounter rate of an individual shrimp with flounder increased dramatically with increasing fish size, irrespective of temperature (Fig. 2*a*). The susceptibility of flounder to shrimp predation (product of P_A, P_C, and P_I) generally decreased with increasing fish size until flounder attained a refuge at 24 mm TL (Fig. 2*a*). Tem-

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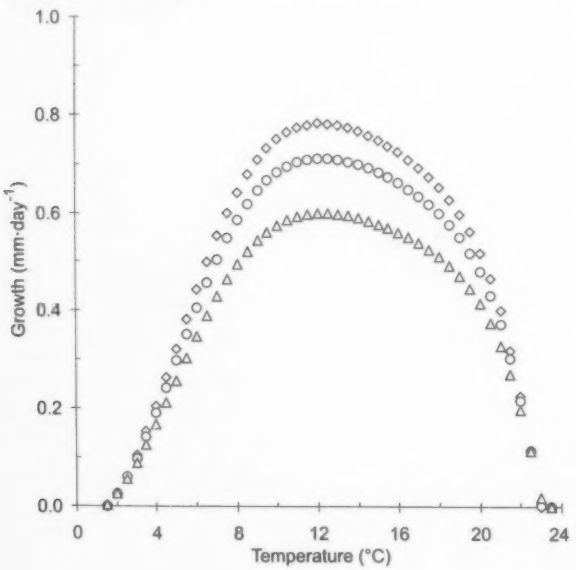
Table 2. Seasonally averaged water temperature (°C) from day 90 to day 190, winter flounder (*Pseudopleuronectes americanus*) juvenile abundance (number of juveniles·100 m^{-2}) and juvenile size (mm total length ± standard deviation), and flounder larval abundance (number of larvae·100 m^{-3}) measured in Narragansett Bay, Rhode Island (1988–2001) and Niantic River, Connecticut (1983–2001).

	Narragansett Bay, Rhode Island				Niantic River, Connecticut			
Year	Water temperature	Juvenile abundance	Juvenile size (sampling date)	Larval abundance	Water temperature	Juvenile abundance	Juvenile size (sampling date)	Larval abundance
1983	—	—	—	—	15.4	55	26.3±7.9 (162)	23.3
1984	—	—	—	—	16.4	31	25.0±5.1 (162)	30.1
1985	—	—	—	—	18.4	24	25.6±6.1 (160)	57.2
1986	—	—	—	—	16.4	46	27.2±5.0 (160)	11.8
1987	—	—	—	—	16.9	73	25.9±5.5 (158)	27.8
1988	12.9	27	55.7±10.4 (186)	15.0	16.2	84	34.0±7.2 (164)	107.5
1989	13.4	52	46.7±8.1 (172)	39.9	16.5	23	28.9±6.3 (162)	84.7
1990	14.1	179	46.3±10.0 (170)	18.5	15.2	188	31.1±8.0 (161)	29.5
1991	12.8	42	56.6±8.5 (170)	17.5	14.8	96	36.5±8.6 (156)	23.0
1992	15.7	198	50.2±7.8 (179)	74.9	16.4	137	27.9±6.5 (163)	62.8
1993	12.6	15	35.9±11.5 (162)	16.6	16.1	13	26.4±5.2 (160)	8.2
1994	15.0	8	42.1±5.4 (169)	15.0	17.5	213	22.6±3.5 (158)	33.6
1995	15.1	40	43.2±6.9 (161)	45.1	17.8	170	29.5±5.6 (157)	71.5
1996	13.4	56	38.0±11.5 (178)	8.3	18.3	25	17.7±5.5 (157)	48.4
1997	13.3	17	43.1±7.5 (164)	28.4	15.4	61	26.8±8.1 (155)	114.8
1998	14.1	14	38.3±8.5 (164)	7.8	16.7	76	19.5±8.6 (152)	58.7
1999	13.3	66	54.6±11.2 (177)	15.1	16.7	71	28.0±9.8 (159)	27.2
2000	15.8	396	43.6±7.7 (174)	6.2	18.7	66	22.9±7.7 (160)	23.3
2001	14.4	74	40.0±8.9 (166)	16.2	16.9	268	19.6±9.9 (157)	34.1
Average	14.0	85	45.3±8.9 (171)	23.2	16.7	90	26.4±6.8 (159)	46.2

Fig. 1. Daily growth rates for 8 mm (△), 16 mm (○), and 24 mm (◇) juvenile winter flounder (*Pseudopleuronectes americanus*) measured as total length increase (mm·day^{-1}) and as a function of water temperature (°C). Values were obtained from a temperature- and weight-specific bioenergetic model described by Rose et al. (1996).



perature had a prominent effect on the susceptibility response curve, whereby increasing temperature increased the overall susceptibility of flounder to shrimp predation. The rate of increase in flounder susceptibility at higher temperatures, however, was not constant across flounder size. Increasing temperature resulted in a disproportionate increase in the susceptibility of medium-sized flounder to shrimp predation, such that the susceptibility response curve was dome-shaped at the highest temperature (15 °C) (Fig. 2*a*). The product of size-dependent encounter rates and susceptibility defines the gross vulnerability of prey. The gross vulnerability of flounder to shrimp predation (number of flounder eaten·$shrimp^{-1}$·m^{-2}·h^{-1}) was dome-shaped across all simulated temperatures when analyzed graphically with respect to prey size (prey density fixed at 2 flounder·m^{-2}) (Fig. 2*b*). The number of flounder consumed and the convexity of the vulnerability response curve increased substantially with increasing temperature. The peak consumption rate of an individual shrimp occurred when preying on a flounder body size of 16.0 mm TL and the number of flounder eaten increased 9.5-fold with an increase in temperature from 5 to 15 °C (Fig. 2*b*).

Model simulations

Simulation I varied flounder growth by ±25% and ±50% per day from the calculated mean growth. Resulting growth rates ranged between 0.31 and 0.66 mm·day^{-1} (±50% growth·day^{-1}), causing the mortality window to range from a maximum of 53 days to a minimum of 25 days (Table 3). The shortened mortality window for faster-growing flounder resulted in these individuals being exposed to cooler temperatures (6.52 °C) and reduced predator densities (0.38 shrimp·m^{-2}) relative to slow

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Table 3. Results of baseline and four model simulations predicting the average daily instantaneous mortality (Z) and cumulative mortality (M) of postsettled winter flounder (*Pseudopleuronectes americanus*) as a function of the period over which flounder are vulnerable to sand shrimp (*Crangon septemspinosa*) predation, i.e., mortality window (MW; days), flounder growth (G; mm·day^{-1}), water temperature (T; °C), and shrimp density (ρ_s; number of shrimp·m^{-2}).

	MW	G	T	ρ_s	Z	M
Baseline simulation	33	0.50	7.32	0.63	0.0111	0.4511
Simulation I						
+50% of daily growth	25	0.66	6.52	0.38	0.0059	0.2057
+25% of daily growth	28	0.59	6.83	0.49	0.0078	0.2953
–25% of daily growth	41	0.42	7.81	0.76	0.0205	0.7611
–50% of daily growth	53	0.31	8.82	0.97	0.1252	1.000
Simulation II						
+4 °C of mean temperature	24	0.67	10.60	0.41	0.0123	0.4332
+2 °C of mean temperature	27	0.61	8.84	0.49	0.0106	0.3937
–2 °C of mean temperature	43	0.38	6.06	0.81	0.0134	0.5751
–4 °C of mean temperature	56	0.30	5.07	1.01	0.0155	0.6958
Simulation IIIA						
14-day early settlement	43	0.38	5.95	0.34	0.0060	0.3152
14-day late settlement	27	0.61	9.00	1.11	0.0256	0.7225
Simulation IIIB						
14-day early settlement	33	0.50	7.32	0.15	0.0024	0.1154
14-day late settlement	33	0.50	7.32	1.22	0.0197	0.6611
Simulation IVA						
14-day early migration	33	0.50	7.32	1.22	0.0192	0.6523
14-day late migration	33	0.50	7.32	0.16	0.0025	0.1211
Simulation IVB						
14-day early migration	33	0.50	7.32	0.63	0.0110	0.4422
14-day late migration	33	0.50	7.32	0.63	0.0106	0.4306

Note: Listed values (except M) represent daily averages estimated from 31 March (day 90) to the end of the respective mortality window.

growers (T = 8.82 °C and ρ_s = 0.97 shrimp·m^{-2}). Consequently, variations in flounder growth had a marked effect on the number of fish surviving beyond the mortality window (Fig. 3*a*). The fastest growers experienced 80% survival at the conclusion of the predation period, whereas slow-growing flounder (0.31 mm·day^{-1}) had no survivors (Table 3). Faster-growing flounder, however, did not have a survival advantage throughout the entire mortality window (Fig. 4*a*). At 20 days after settlement, cumulative mortality was greatest for flounder growing at 0.68 mm·day^{-1} (M = 11.7%). In comparison, flounder growing less than 0.38 mm·day^{-1} did not experience any mortality because of their small size and very low encounter rates with shrimp (i.e., slow growers initially have low vulnerability despite high susceptibility) (Fig. 2). Flounder growing at an average rate of 0.90 mm·day^{-1} or more reached a size refuge (>24 mm TL) by 20 days after settlement and therefore experienced no further mortality from shrimp predation (Fig. 4*a*). Beyond 20 days after settlement, slow-growing flounder began to suffer high rates of predation as these individuals grew into the mortality window (i.e., >12 mm TL owing to size-dependent E; Fig. 2). For example, flounder growing at rates of 0.30 mm·day^{-1} experienced no mortality for the first 20 days after settlement. However, 20 days later (40 days after settlement), the same individuals suffered 73% mortality, and by 60 days after settlement, there were no survivors (Fig. 4*a*). Thus, the initial survival advantage of slow growth, and consequently being small-at-age, was lost as these flounder eventually grew into a vulnerable size and remained within the mortality window for an extended period of time.

Variations in temperature had an appreciable effect on flounder survival (Fig. 3*b*). Flounder exposed to cold temperatures (–2 and –4 °C) suffered higher mortality rates than those fish exposed to mean and warm (+2 and +4 °C) temperatures (Table 3). Warm temperatures promote faster growth, which in turn reduces the amount of time that flounder are vulnerable to shrimp predation. For example, flounder exposed to a 4 °C increase in mean temperature (average T during MW = 10.60 °C) had growth rates of 0.67 mm·day^{-1} and a mortality window of 24 days, whereas fish exposed to the coldest temperature (average T during MW = 5.07 °C) grew at 0.30 mm·day^{-1} and were vulnerable to shrimp predation for 56 days (Table 3). As a consequence of the mortality window ending earlier in the season, fast-growing flounder also benefitted from reduced predator densities (ρ_s at ±4 °C = 0.41 and 1.01 shrimp·m^{-2}, respectively). The combination of these factors (fast G, shortened MW, and reduced ρ_s) resulted in flounder experiencing a 61% decrease in mortality at the warmest temperature (+4 °C) relative to the coldest temperature (–4 °C). Increased temperature beyond an optimal level, however, is detrimental to flounder survival. Postsettled flounder growth, for example, is depressed at temperatures greater than 12.2 °C (Fig. 1). Moreover, the effect of temperature on shrimp predatory behavior (i.e., predation sequence) is a key factor determining flounder

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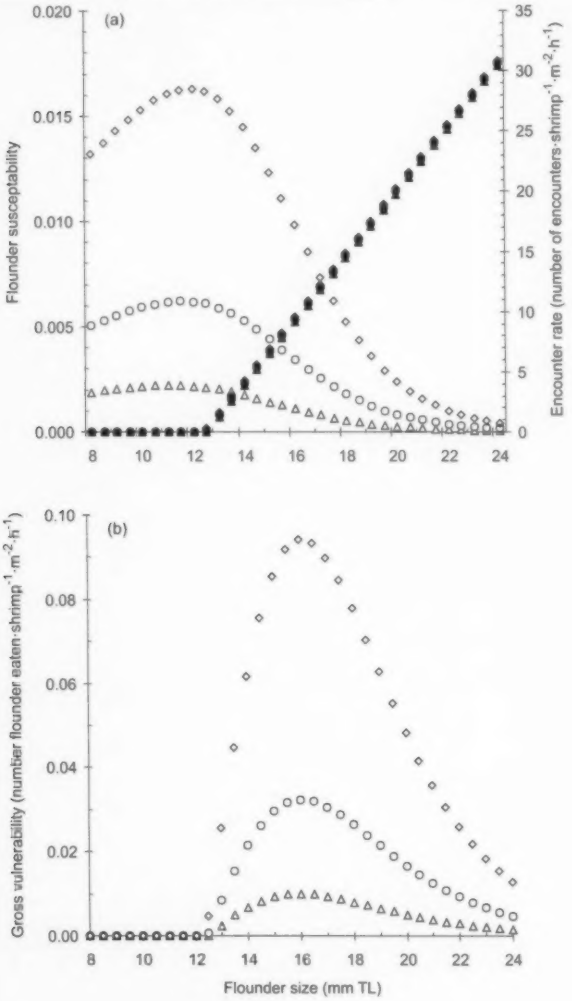
Fig. 2. (*a*) Juvenile winter flounder (*Pseudopleuronectes americanus*) size-dependent (mm total length (TL)) susceptibility (open shapes; primary *y*-axis) and encounter rate (number of encounters·shrimp^{-1}·m^{-2}·h^{-1}) (solid shapes; secondary *y*-axis) with sand shrimp (*Crangon septemspinosa*). (*b*) Flounder size-dependent (mm TL) gross vulnerability (number of flounder eaten·shrimp^{-1}·m^{-2}·h^{-1}) to shrimp predation. Susceptibility, encounters, and gross vulnerability were evaluated at three temperatures: 5 °C (△), 10 °C (○), and 15 °C (◇).



mortality. Despite faster growth (0.67 mm·day^{-1}) and a reduced mortality window (24 days), flounder exposed to a 4 °C increase in mean water temperature suffered a 10% increase in cumulative mortality compared with those fish exposed to a 2 °C daily increase in temperature (G = 0.61 mm·day^{-1} and MW = 27 days at the +2 °C treatment). This was attributed to the increased susceptibility of flounder to shrimp predation at warmer temperatures (Fig. 2*a*). Initially, after settlement, cooler temperatures minimized flounder mortality (20 and 40 days after settlement) (Fig. 4*b*). Cold temperatures promote slow growth (Fig. 1), and flounder that are small-at-age experience reduced shrimp encounters, which decreases the gross vulnerability of fish to shrimp predation (Fig. 2). In time, however, slow growers reach vulnerable sizes (>12 mm TL) and suffer extensive mortality. The lowest cumulative mortality for a single cohort at the end of the mortality window (60 days after settlement) occurred when the average temperature was 11.8 °C (Fig. 4*b*). Below the optimal temperature, mortality was increased owing to slow growth and a prolonged mortality window. Above the optimal temperature, flounder suffered higher mortality because of intensified predation and an increased susceptibility to predatory shrimp (Fig. 2*a*).

Early settlement resulted in reduced mortality and higher survivorship of the flounder cohort (Figs. 3*c*, 3*d*). Flounder settling 14 days early in simulations IIIA and IIIB experienced cumulative mortality rates of 31.5% and 11.5%, respectively (Table 3). In contrast, flounder settling later in the season had higher rates of mortality; M for simulations IIIA and IIIB was 72.3% and 66.1%, respectively. For simulation IIIB, decreased survival rates later in the spring season were a result of higher shrimp densities (0.15 and 1.22 shrimp·m^{-2} for early and late settlement, respectively). Late settlers in simulation IIIA also suffered greater mortality as a result of higher predator density. Additionally, mortality rates for both early and late settlers were greater in simulation IIIA, relative to IIIB, as a result of differences in temperature (Table 3). Early settlers in simulation IIIA were exposed to colder temperatures, which decreased flounder growth and extended the length of the mortality window. Conversely, late settlers in simulation IIIA were exposed to warmer temperatures (relative to simulation IIIB), which further decreased the survival of flounder owing to enhanced predation intensity.

Simulation IVA predicted that a delay in shrimp migration resulted in a higher number of flounder surviving beyond the mortality window (Fig. 3*e*). In contrast, early predator migration resulted in greater shrimp densities at flounder settlement (1.22 shrimp·m^{-2}) and therefore a higher rate of cumulative mortality (65.2%; Table 3). Thus, predictions generated from simulations that altered shrimp migrations (simulation IVA) produced similar results to simulations that examined the effect of different times of flounder settlement on mortality rates (simulation IIIB). In both situations, differences in flounder mortality were attributed to the existing shrimp density. Simulation III determined that early flounder settlement resulted in reduced mortality and higher survivorship (Table 3; Figs. 3*c*, 3*d*). The primary factor contributing to the enhanced survivorship of flounder was reduced shrimp density. The spatial and temporal refuge obtained by early settlement, however, was lost when shrimp migration also occurred at an early date. Simulation IVB predicted that situations in which predator migration and flounder settlement events occur together, flounder mortality rates were relatively constant across treatments and therefore could be modeled by baseline simulations (Fig. 3*f*).

Field sampling and comparisons with model outputs

Seasonally averaged water temperature (day 90 to day 190) was colder in Narragansett Bay (average = 14.0 °C) than in Niantic River (average = 16.7 °C) (Table 2). Estimates of juvenile winter flounder abundance from late spring field sampling indicated that flounder numbers were comparable

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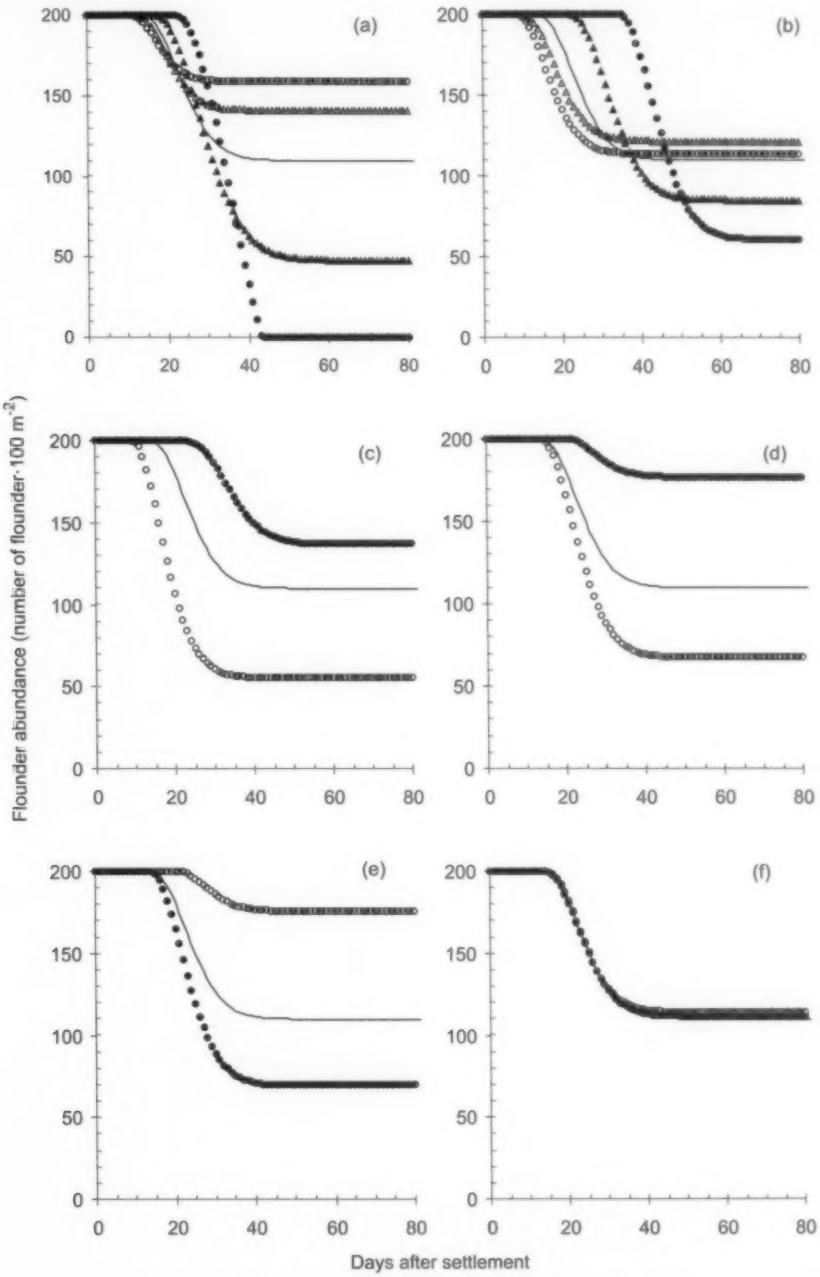
Fig. 3. Results of model simulations estimating juvenile winter flounder (*Pseudopleuronectes americanus*) abundance (number of flounder·100 m^{-2}) as cohorts were subjected to sand shrimp (*Crangon septemspinosa*) predation. (*a*) Flounder growth (simulation I): mean daily growth, solid line; ±25% mean daily growth, △ and ▲, respectively; ±50% mean daily growth, ○ and ●, respectively. (*b*) Temperature (simulation II): mean daily temperature, solid line; ±2 °C mean daily temperature, △ and ▲, respectively; ±4 °C mean daily temperature, ○ and ●, respectively. (*c* and *d*) Flounder settlement (simulations IIIA and IIIB): mean settlement date (day 90), = solid line; 14 days early, ●; 14 days late, ○. (*e* and *f*) Shrimp migration (simulations IVA and IVB): mean migration, solid line; 14 days early, ●; 14 days late, ○.



between Narragansett Bay and Niantic River (85 versus 90 juveniles·100 m^{-2}) (Table 2). The body size of juvenile flounder measured during field sampling was considerably smaller in Niantic River (26.4 ± 6.8 mm TL) relative to Narragansett Bay (45.3 ± 8.9 mm TL) (Table 2), but this discrepancy may be partially explained by differences in av-

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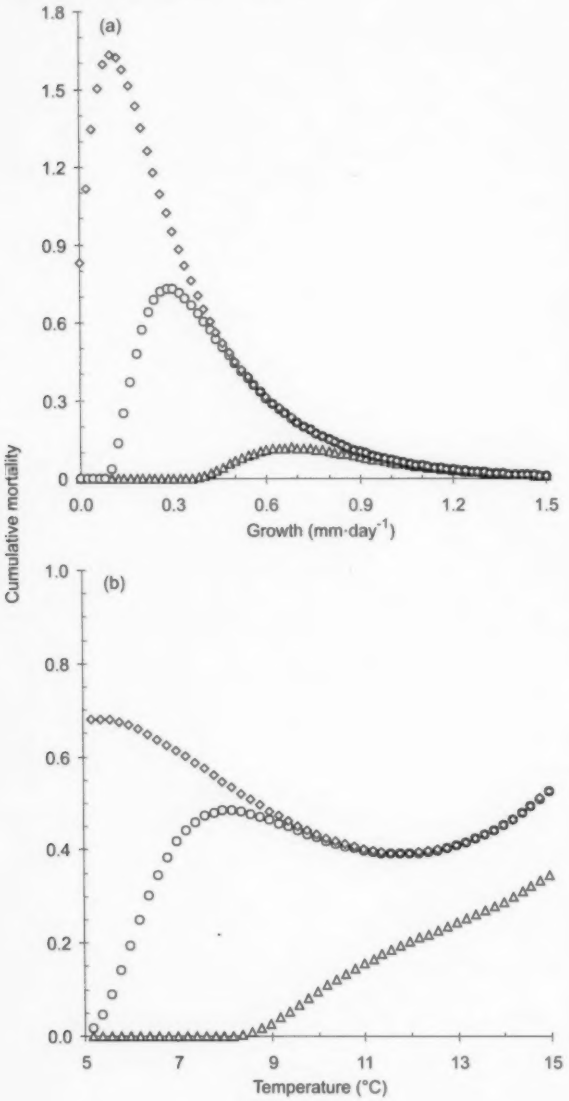
Fig. 4. Juvenile winter flounder (*Pseudopleuronectes americanus*) cumulative mortality from sand shrimp (*Crangon septemspinosa*) predation as a function of flounder growth (mm·day^{-1}) and seasonally averaged water temperature (°C) from day 90 to day 150. Cumulative mortality was evaluated at 20 days (△), 40 days (○), and 60 days after settlement (◇).



erage sampling date (day 159 and day 171 for Niantic River and Narragansett Bay, respectively) and sampling gear (beam trawl and beach seine for Niantic River and Narragansett Bay, respectively) (Van der Veer et al. 1997). Reported abundance of larval winter flounder was lower in Narragansett Bay than in Niantic River (23.2 versus 46.2 larvae·100 m^{-3}) (Table 2).

The average flounder settling density was assumed to be 600 flounder·100 m^{-2} for Narragansett Bay and Niantic River (three cohorts at 200 flounder·100 m^{-2}). Initial cohort sizes varied interannually, however, and were scaled according to reported estimates of flounder larval abundance (Table 2). The range of flounder settling densities for Narragansett Bay and Niantic River were 162–1938 and 156–1494 flounder·100 m^{-2}, respectively. Flounder settlement occurred earlier in the year in Narragansett Bay (average settlement date = 106.4 ± 2.1 to 128.8 ± 2.1 for first and third cohort, respectively) as compared with Niantic River (average settlement date = 122.4 ± 1.5 to 140.0 ± 1.4 for first and third cohort, respectively). The predicted cumulative mortality of juvenile flounder was comparable between Narragansett Bay (average M = 66.6 ± 4.2%; range M = 40.9–93.8%) and Niantic River (average M = 61.1 ± 5.2%; range M = 17.3–92.7%). The average cumulative mortality of juvenile flounder across years and regions was 63.3 ± 3.2%.

There was no significant association between the number of postsettled flounder predicted to survive beyond the mortality window and the observed flounder abundance sampled annually in Narragansett Bay and Niantic River during late May to June (Kendall's τ = 0.0911, p = 0.4569, n = 33). An additional model simulation was run to examine the cumulative survival (S) of three flounder cohorts having a fixed density of 200 flounder·100 m^{-2}·cohort^{-1} and settlement dates of 90, 110, and 120 days (cohorts 1, 2, and 3, respectively). Cumulative survival (S = 1 – M) was calculated from the previously discussed deterministic model and was evaluated over a continuous range of seasonally averaged temperatures (range = 12.0 to 20.0 °C evaluated at 0.01 °C increments) (Fig. 5). Seasonal temperature was averaged from day 90 to day 190, the approximate residence time of predatory shrimp in flounder settling grounds (eq. 6). Flounder predicted cumulative survival was dome-shaped with respect to seasonally averaged temperature (Fig. 5). Maximum survival occurred at 16.1 °C and decreased at an accelerated rate above and below this optimal temperature. Juvenile flounder abundance, measured annually in Narragansett Bay and Niantic River, was also analyzed with respect to temperature (Fig. 5). Similar to model predictions of flounder cumulative survival, juvenile abundance measured in the field was dome-shaped with respect to seasonally averaged temperature such that maximum abundance occurred at 16.5 °C and decreased considerably at colder and warmer temperatures. There was a positive association between model-predicted estimates of flounder cumulative survival and flounder abundance measured in the field (Kendall's τ = 0.1918), but this relationship was insignificant (p = 0.1175, n = 33).

The predicted number of flounder consumed by shrimp (based on interannual variations in daily temperature, initial cohort size and settling date, and shrimp migration) increased at a decelerating rate with increasing flounder settling density until reaching an upper asymptote at ~1000 flounder· 100 m^{-2} (Fig. 6*a*). The number of flounder dying between initial settlement and observed abundances in late May to June in Narragansett Bay and Niantic River initially increased at an accelerated rate with increasing flounder settling density until passing an inflection point (~600 flounder·100 m^{-2}), beyond which mortality increased at a decelerating rate (Fig. 6*b*). The presence of density-dependent mortality was determined by testing for a significant correlation between predicted and observed mortality and the natural logarithm of flounder settling density. Density-dependent mortality was evident for

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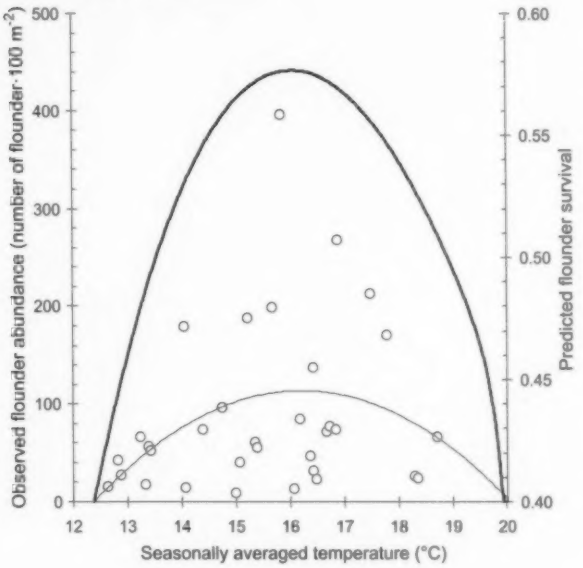
Fig. 5. Juvenile winter flounder (*Pseudopleuronectes americanus*) interannual abundance (number of flounder·100 m^{-2}) (○; primary *y*-axis) estimated in Narragansett Bay, Rhode Island (1988–2001), and Niantic River, Connecticut (1983–2001), during late May and June. A second-order polynomial (thin line; primary *y*-axis) was fit to abundance data by least-squares analysis (Abundance = $-4.856T^2 + 160.55T - 1229.4$, where T is the seasonally averaged temperature (°C) from day 90 to day 190). The predicted cumulative survival ($S = 1 - M$) of flounder (thick line; secondary *y*-axis) as a function of seasonally averaged temperature is also presented.



model predictions and observations from field sampling in Narragansett Bay and Niantic River (predicted: $R^2 = 0.5284$, $F = 33.62$, df = 1,31, $p < 0.001$; observed: $R^2 = 0.1948$, $F = 7.26$, df = 1,31, $p < 0.05$). The pattern of density dependence, however, was markedly different between predicted and observed mortality (Figs. 6*c*, 6*d*). The model predicted that flounder mortality caused by shrimp predation was inversely density-dependent, indicating depensation as instantaneous mortality significantly decreased with increasing flounder density (Fig. 6*c*). Conversely, observed flounder mortality between initial settlement and late spring was density-dependent, suggesting compensation and an increase in instantaneous mortality at greater flounder densities (Fig. 6*d*).

Discussion

Climatic change over the last 40 years that has increased water temperature in temperate estuaries may be a critical factor determining the survival of winter flounder. In a study examining the mechanisms altering the recruitment success of the North Sea plaice (*Pleuronectes platessa*), Van der Veer et al. (1990) determined that juvenile plaice survival was highly dependent on water temperature. Those fish inhabiting estuaries with warmer spring water temperature suffered greater predator-induced mortality from the brown shrimp (*Crangon crangon*) than those estuaries that maintained colder spring temperature. A predator–prey interaction similar to the one occurring between brown shrimp and juvenile plaice exists in Northwest Atlantic estuaries between recently settled winter flounder and the sand shrimp *C. septemspinosa*. Consequently, increasing water temperature and its effect on trophic dynamics could account for the continual decline of localized winter flounder populations. The purpose of this study was to examine the implications of warming spring water temperature on the survival of winter flounder by integrating the temperature-mediated responses of both juvenile flounder and *C. septemspinosa*.

The relative magnitude of crangonid shrimp predation on flatfish is influenced greatly by prey body size (Van der Veer et al. 1990; Gibson et al. 1995; Witting and Able 1995). Although it is apparent that susceptibility to predation decreases monotonically with increasing prey size, the actual vulnerability of prey is more complicated (Cowan et al. 1997). Several investigators, for instance, have cautioned that forecasting the survival of early-staged fish, strictly as a function of susceptibility, may lead to erroneous conclusions because of the added effect of size-dependent encounter rates on the predation outcome (Litvak and Leggett 1992; Pepin et al. 1992; Paradis et al. 1996). Juvenile winter flounder that are large have increased encounter rates with *C. septemspinosa* because they are more conspicuous and active than smaller conspecifics (Taylor 2003). Thus, the combined effect of susceptibility and size-dependent encounters between flatfish and predatory shrimp (i.e., gross vulnerability) results in a mortality curve that is dome-shaped with respect to flounder size. At the extremes of the dome-shaped vulnerability curve, shrimp consume relatively few small and large flounder. Small flounder (8–12 mm TL) have an immediate survival advantage because of their inconspicuousness to predatory shrimp. Small body sizes and associated decreases in activity cause a significant reduction in encounters with predators, thus minimizing the prey's gross vulnerability. Large flounder (>17 mm TL), despite frequent encounters with shrimp, also experience increased survival because of their superior escape capabilities and the prolonged handling time of predators (Gibson et al. 1995; Taylor 2003). Conversely, medium-sized flounder suffer the highest rates of instantaneous mortality. These results are consistent with those of several other investigators that suggested that early-staged fish preyed on by ambush raptorial invertebrates exhibit vulnerability curves that are dome-shaped (Bailey and Houde 1989; Litvak and Leggett 1992).

Small body sizes, relative to intermediate sizes, in certain situations can reduce instantaneous mortality. The immediate disadvantage imposed to larger flounder, however, may be compensated over the long term by these individuals having faster growth rates. The results from this study clearly demonstrate that small (within-year) growth variations of a cohort can have a profound effect on juvenile flounder survival. Cohorts of faster-growing individuals had a higher survival rate than slower-growing cohorts. The main benefit of accelerated growth is the decreased time that flounder are susceptible to *C. septemspinosa* predation. As a consequence of the mortality window ending earlier in the season, fast-growing flounder also benefit from reduced shrimp densities and cooler temperatures, which in turn decreases predation intensity. Consequently, the initial advantage of being small-at-age

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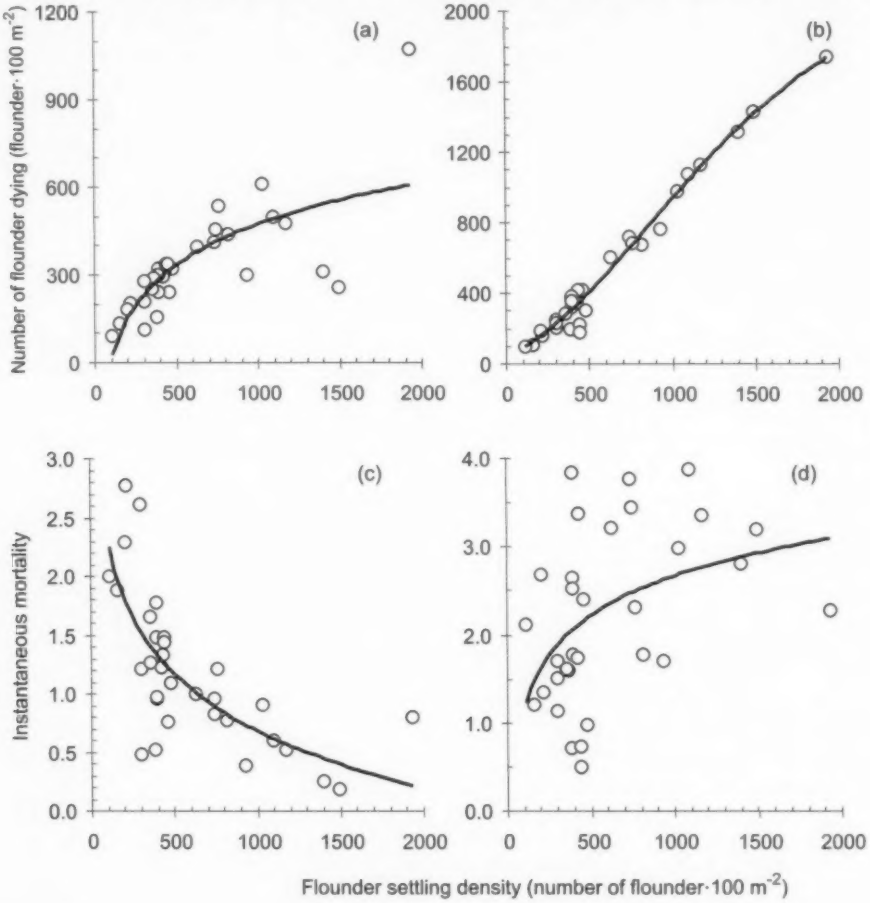
Fig. 6. Number of juvenile winter flounder (*Pseudopleuronectes americanus*) dying from (*a*) initial settlement to the end of the modeled mortality window and (*b*) late spring and summer field sampling in Narragansett Bay, Rhode Island (1988–2001), and Niantic River, Connecticut (1983–2001). (*c*) Flounder instantaneous mortality rates predicted from model simulations and (*d*) observed field abundances in Narragansett Bay and Niantic River. Estimates of instantaneous mortality rates for model-predicted data were calculated as the difference in natural logarithm of abundance between initial flounder settling density and the predicted flounder abundance at the end of the mortality window. Estimates of instantaneous mortality rates for field data were calculated as the difference in natural logarithm of abundance between initial flounder settling density and the observed flounder abundance during field sampling in late May to June.



due to slow growth rates is negated once flounder grow into a more vulnerable size class and remain susceptible to predation for an extended length of time. When the residence time of predators exceeds the length of the mortality window (e.g., shrimp predation on juvenile flounder), predation will likely become negatively size-dependent over time and faster-growing individuals incur a survival advantage. Situations can occur, however, when the presence of predators does not coincide temporally with the full developmental period of the early juvenile life stage (Paradis et al. 1999). Transient predators (e.g., piscivorous fish) that feed during restricted periods of the mortality window can preclude the advantages of fast growth if larger individuals are selectively consumed during the brief predation period (Paradis et al. 1999).

Elevated temperatures in Northwest Atlantic estuaries during the early spring potentially increase juvenile flounder survival by accelerating growth and limiting the time that fish are vulnerable to *C. septemspinosa* predation. Extreme temperature increases, however, can depress flounder growth because a disproportionate amount of energy is devoted to increased metabolism, thereby reducing energy for somatic development (Rose et al. 1996). Increased temperatures above optimal levels reduce flounder growth, hence prolonging the mortality window and increasing predator-induced mortality. Moreover, flounder survival is also reduced during anomalous warm years because of the concurrent effect of increased temperature on *C. septemspinosa* predatory behavior. Results from this study suggest that maximum survival of juvenile flounder occurs at an average seasonal temperature of 16.1 °C. Temperatures above this optimal level intensify flounder mortality because of an increased susceptibility to shrimp predation. Similarly, juvenile flounder exposed to temperatures below 16.1 °C

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experienced high mortality. In contrast to warm conditions, flounder exposed to cold temperatures benefit from reduced predator activity. Mortality of flounder is still substantial, however, because of slow growth rates and, consequently, a prolonged time period over which fish were vulnerable to shrimp predators.

Water temperature is a key component underlying the predator–prey dynamics between *C. septemspinosa* and juvenile winter flounder. Taylor and Collie (2003) found that postsettled winter flounder benefit from a low prey density refuge at 10 °C because of a stabilizing and density-dependent, type-III functional response of predatory sand shrimp. Increasing water temperature to 16 °C, however, destabilizes the predator–prey interaction as shrimp switch their feeding behavior to an inversely density-dependent, type-II response. Consequently, warmer temperatures preclude a low prey density refuge for flounder, and thus sand shrimp have the capacity to drive prey populations to local extinction. In this study, there was evidence of depensation as flounder mortality decreased significantly with increasing fish settling density. If elevated temperatures intensify levels of depensation, the warming trend in temperate estuaries could decrease the resiliency of flounder populations to natural or anthropogenic perturbations.

The relative abundance and distribution of juvenile winter flounder and *C. septemspinosa* obviously affect the predator–prey interaction. The two primary factors controlling the spatial and temporal overlap between *C. septemspinosa* and juvenile winter flounder and their relative densities are (1) shrimp migration from deep to shallow water and (2) winter flounder metamorphosis and subsequent settlement to the benthos. The timing of larval winter flounder metamorphosis is controlled primarily by temperature (Laurence 1975; Chambers and Leggett 1987; Sogard et al. 2001). Elevated temperatures increase the rate of larval flounder development and thus induce an earlier settlement. Chambers and Leggett (1987), for example, confirmed that the timing of winter flounder metamorphosis and settlement was length- and not age-dependent. Moreover, Sogard et al. (2001) observed that later larval occurrence and corresponding later metamorphosis and settlement of winter flounder was intrinsically linked to colder water temperatures. As such, those mechanisms that alter the growth rate of larval winter flounder, such as temperature, are the controlling factors regulating fish settlement. Results from this study suggest that a survival advantage was incurred by winter flounder settling early in the spring season because of lower predator densities. These results could again lead to the assumption that the warming trend observed in Northwest Atlantic estuaries imparts a survival advantage to young-of-the-year winter flounder. Elevated water temperatures increase larval winter flounder growth, which in turn induces earlier settlement, and flounder then benefit from a low predator density refuge. Recent increases in water temperature, however, are likely to impact shrimp migratory behavior as well.

Crangon septemspinosa undergo seasonal onshore migrations, triggered primarily by the increase in spring water temperature. The natural warming of water temperature during spring initiates a return migration of shrimp back to shallow estuaries from deeper water, presumably because these areas provide greater food resources and optimal conditions for reproduction (Haefner 1969, 1979). With the advent of increased spring water temperature occurring earlier in the year, sand shrimp possibly exhibit a premature migration into areas occupied by susceptible, recently metamorphosed winter flounder. As a consequence of this newly formed spatial and temporal overlap between predator and prey, recently settled winter flounder could suffer extensive shrimp-induced mortality. Results from this study indicate that a premature return migration of sand shrimp into estuarine nursery grounds results in increased mortality of juvenile winter flounder, primarily as a result of higher shrimp density during flounder settlement. Furthermore, the apparent low predator density refuge achieved by early-settling flounder is negated when shrimp arrive in shallow estuarine habitats earlier in the spring season.

Predator-induced mortality calculated in this study agreed with other published estimates of crangonid shrimp predation on newly settled flatfish. According to model simulations, *C. septemspinosa* consume 17–94% (average = 63.3 ± 3.2%) of the total number of flounder settling to the benthos. Van der Veer and Bergman (1987) estimated that the shrimp *C. crangon* accounted for 40% of the observed mortality in juvenile plaice, *P. platessa*, per month. Through the development of an individual-based model, Burrows et al. (2001) investigated the size-dependent predation by *C. crangon* on populations of newly settled 0-group plaice. The individual-based model predicted plaice daily instantaneous mortality to be 0.0028–0.0161 (average = 0.0094), and 80% of the variance in predicted mortality was attributed to differences in *C. crangon* population density. Model-based predictions were then compared with 7 years of catch data for juvenile plaice from Ardmucknish Bay, located on the western coast of Scotland. Accordingly, predicted shrimp-induced mortality accounted for 18%–100% (average = 61%) of the total observed plaice daily mortality (Burrows et al. 2001).

Predicted flounder abundance and cumulative survival were statistically unrelated to observed flounder abundance sampled annually in Narragansett Bay and Niantic River during late May to June. The failure of the model to predict interannual variations in postsettled flounder may be attributed to several fundamental assumptions of the model. Predatory *C. septemspinosa* did not grow during the specified predation period (mortality window), and thus predator size was held constant. Moreover, any shrimp deemed large enough to prey upon postsettled winter flounder (>40 mm) had the same probability of successfully consuming a given-sized winter flounder. Allowing for predator growth throughout the model simulation increases shrimp density over time, as new individuals are added to the predatory population once attaining a size greater than 40 mm. An increase in predator body size also corresponds to an increase in the capability of capturing, subduing, and successfully consuming prey (Van der Veer and Bergman 1987). Therefore, permitting predator growth over time would likely increase predation intensity owing to an increase in predator body size and density. One plausible mechanism that could reduce predation as time progressed is if juvenile winter flounder growth far exceeded that of sand shrimp, effectively minimizing the predator–prey size ratio (Paradis et al. 1996).

A second key assumption of the model was that winter flounder mortality was due entirely to *C. septemspinosa* pre-

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dation. Other mortality factors, such as additional predators on young flounder, could mask the effects of sand shrimp regulation of juvenile winter flounder populations and year-class strength. Based on laboratory feeding experiments, Fairchild and Howell (2000) implicated the green crab (*Carcinus maenas*) as a potential source of mortality for recently settled winter flounder. Winter flounder otoliths were also identified in the regurgitated pellets of the double-crested cormorant (*Phalacrocorax auritus*) (DNC 2002). Cormorant predation has depleted juvenile winter flounder populations close to known nesting colonies, with higher fish densities occurring beyond the foraging range of this avian piscivore (DNC 2002). A variety of fish species have also been implicated as potential predators of young winter flounder, including summer flounder (*Paralichthys dentatus*) (Manderson et al. 2000), striped searobin (*Prionotus evolans*) (Manderson et al. 1999), and grubby sculpin (*Myoxocephalus aenaeus*) (DNC 2002).

The deterministic model relies on the unrealistic assumption that the density of *C. septemspinosa* remains constant across years. The predicted density of *C. septemspinosa* used in model simulations was calculated from observed abundance of shrimp from field surveys in Narragansett Bay in 2001. The corresponding density of shrimp during the spring and early summer were held constant across model simulations. Shrimp density, however, potentially exhibits wide annual variations, primarily in association with previous winter conditions. *Crangon septemspinosa* seek deep water over cold winter months, remaining quiescent and buried in the sediment. Significant mortality may occur to dormant shrimp at this time when water temperatures approach 0 °C (Haefner 1979). Thus, as a result of physiological limitations, near-freezing water temperatures appear to be an important mechanism regulating shrimp populations. Annual fluctuations in winter conditions are expected to have dramatic effects on the mortality of overwintering populations of sand shrimp and thus their relative densities during shoreward migrations in spring. This in turn influences the survival of winter flounder cohorts established the same year. Winter water temperature is believed to indirectly influence plaice *P. platessa* recruitment by affecting the spatial distribution and overall survival of overwintering predatory *C. crangon* populations (Van der Veer et al. 1990, 2000). *Pleuronectes platessa* was found to have highly successful recruitment classes following a winter with cold water temperature. The enhanced survivorship of newly settled plaice was attributed to a reduction or absence of *C. crangon* predators, where decreased winter water temperature minimized shrimp numbers by inducing heavy mortality or forcing the crustaceans to migrate to deeper water (Van der Veer et al. 2000).

Juvenile winter flounder mortality in Niantic River is strongly correlated to the previous winter water temperatures. Since 1984, the five years exhibiting the greatest calculated daily instantaneous mortality of postsettled winter flounder were also years in which the preceding February water temperatures were above average (DNC 2002). The increased mortality of postsettled winter flounder in years of warmer winter temperatures may be attributed to an increased survivorship of overwintering populations of sand shrimp. This phenomenon would not be detected, however, in the current model because annual predator density was held constant and predicted mortality rates of postsettled winter flounder were based solely on spring, and not winter, water temperatures.

There is some evidence that the deterministic model presented in this study explains general trends in annual winter flounder year-class success. For example, both predicted and observed flounder abundance was maximal in years when the seasonally averaged temperature was approximately 16 °C. Above and below this temperature, flounder year-class size was considerably lower, possibly as a result of the effect of temperature on trophic dynamics. Factors that contribute to low sand shrimp predation may be a necessary element for high juvenile winter flounder recruitment into the adult population. These factors, however, are not always sufficient in establishing strong year-classes, given that low juvenile winter flounder abundance also co-occurs with high-predicted cumulative survival. In such cases, other mortality factors are likely exerting a negative influence on flounder survival. Similar effects have been observed in other fish species. In an analysis of larval pollock (*Pollachius virens*) and haddock (*Melanogrammus aeglefinus*) growth and its impact on survival, Fortier and Quiñonez-Velazquez (1998) demonstrated that low growth performance resulted in low survival and high growth performance resulted in variable survival. The unexpected observation of low survival at high growth performance indicated that fast growth was a necessary but insufficient condition for survival and suggests that factors other than suboptimal growth were reducing the survival of the pollock and haddock cohorts (Fortier and Quiñonez-Velazquez 1998).

Crangon septemspinosa predation is a significant source of mortality on postsettled winter flounder, which warrants further investigation. Additionally, the model presented in this study suggests that increases in water temperature exacerbate the predator-induced mortality of juvenile flounder. Thus, the recent warming trend experienced in Northwest Atlantic estuaries, and its impact on trophic dynamics, may help explain the failure of the winter flounder stocks to recover. Conclusive evidence linking winter flounder recruitment failure to intensified sand shrimp predation as a result of increased water temperature, however, is still lacking.

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The effect of turbulence on the cost of swimming for juvenile Atlantic salmon (*Salmo salar*)[1]

Eva C. Enders, Daniel Boisclair, and André G. Roy

Abstract: Fish activity costs are often estimated by transforming their swimming speed in energy expenditures with respirometry models developed while forcing fish to swim against a flow of constant velocity. Forced swimming models obtained using a procedure that minimizes flow heterogeneity may not represent the costs of swimming in rivers characterized by turbulence and by a wide range of instantaneous flow velocities. We assessed the swimming cost of juvenile Atlantic salmon (*Salmo salar*) in turbulent flows using two means (18 and 23 cm·s^{-1}) and two standard deviations of flow velocity (5 and 8 cm·s^{-1}). Twenty respirometry experiments were conducted at 15 °C with fish averaging 10 g. Our results confirmed that swimming costs are affected by the level of turbulence. For a given mean flow velocity, swimming costs increased 1.3- to 1.6-fold as turbulence increased. Forced swimming models underestimated actual swimming costs in turbulent flow by 1.9- to 4.2-fold. Spontaneous swimming models overestimated the real cost of swimming in turbulent flow by 2.8- to 6.6-fold. Our analyses suggest that models in which both the mean and the standard deviation of flow velocity are explicitly represented are needed to adequately estimate the costs of swimming against turbulent flows.

Résumé : Les coûts d'activité des poissons sont souvent estimés en transformant leur vitesse de nage en dépenses énergétiques avec des modèles respirométriques développés lorsque les poissons nagent contre un écoulement d'une vitesse constante. Cependant, les modèles de nage forcée obtenus en utilisant une procédure qui minimise l'hétérogénéité de l'écoulement peuvent ne pas représenter les coûts de nage dans des rivières caractérisées par une turbulence, et ainsi, par une grande étendue de vitesses instantanées de l'écoulement. Nous avons évalué le coût de la nage de juvéniles du saumon atlantique (*Salmo salar*) dans un écoulement turbulent en utilisant deux moyennes (18 et 23 cm·s^{-1}) et deux écarts types de vitesse de l'écoulement (5 et 8 cm·s^{-1}). Nous avons effectué 20 expériences respirométriques à une température de l'eau de 15 °C avec des poissons d'une masse moyenne de 10 g. Nos résultats ont confirmé que les coûts de la nage sont affectés par les niveaux de turbulence. Pour une vitesse moyenne donnée de l'écoulement, les coûts de la nage ont augmenté par un facteur de 1,3 à 1,6 alors que la turbulence augmente. Les modèles de la nage forcée ont sous-estimé les coûts effectifs de la nage en écoulement turbulent par un facteur de 1,9 à 4,2. Les modèles de la nage spontanée ont sur-estimé les coûts réels de la nage par un facteur de 2,8 à 6,6. Nos analyses suggèrent que des modèles dans lesquels la moyenne et l'écart type de la vitesse de l'écoulement sont représentés de façon explicite sont requis pour estimer les coûts de la nage contre un écoulement turbulent.

Introduction

Bioenergetic models can be applied to quantify fish habitat quality using the net energy gain obtained by a fish under specified environmental conditions (Hayes et al. 2000). In suitable habitats, fish have a positive balance between the energy acquired from their environment and that required for metabolic expenditures and physiological maintenance (Fausch 1984). Bioenergetic modeling involves the estimation of consumption, growth, metabolism, excretion, and egestion. Although activity metabolism is the least understood component of fish bioenergetic models, it has been argued to represent a large and variable proportion of fish energy budget (Boisclair and Leggett 1989; Boisclair and Sirois 1993; Rowan and Rasmussen 1996). Hence, inappropriate assumptions about activity metabolism may have a strong influence on the accuracy of the predictions of net energy gain and habitat quality values generated by bioenergetic models (Ney 1993; Boisclair 2001).

Fish activity metabolism may be estimated by quantifying fish behaviour and transforming the characteristics of fish behaviour (types and numbers of movements) in energy expenditures. This approach has been used to estimate the ac-

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tivity metabolism of fish in lakes (Lucas et al. 1991; Sirois and Boisclair 1995; Briggs and Post 1997). Estimation of activity metabolism for fish living in rivers represents a particular challenge because of the unknown metabolic consequences for fish of having to swim against a turbulent flow (Roy et al. 1999; Boisclair 2001). The cost of performing feeding motions from the riverbed towards the water surface to capture prey items drifting in the water flow is often estimated using forced swimming models (Puckett and Dill 1985; Sabo et al. 1996). These models are obtained using flume respirometers designed to minimize flow heterogeneity (Bainbridge 1958; Brett 1964; Beamish 1978). The experimental conditions used to develop forced swimming models resemble the conditions found in rivers because fish swim against a flow. However, these models focus on steady swimming and do not account for the costs of performing changes of speed and direction. Changes of speed and direction have been suggested to incur a 3- to 22-fold increase in fish respiration rates relative to predictions made by forced swimming models (Boisclair and Tang 1993; Tang et al. 2000). Spontaneous swimming models adequately account for the costs of performing accelerations and turns, but they have been developed and used with fish swimming in absence of flow (Trudel and Boisclair 1996; Aubin-Horth et al. 1999; Tang et al. 2000).

Turbulence is the state of a flow characterized by the superposition of intense small-scale motions in all directions on a main large-scale flow (Vogel 1994). Turbulence may be perceived as a partly random, partly structured, temporal variation of flow velocity at one point in space (Kirkbride 1993). Turbulence may also be perceived as the spatial heterogeneity of flow velocities at a given time (Bradshaw 1985). As such, the description of turbulence depends on the temporal and spatial scales at which it is observed. Turbulence and, in particular, its descriptor, turbulence intensity (standard deviation of the flow velocity divided by the mean flow velocity), may be expected to vary with the temporal scale (e.g., ms or min) used to measure flow velocity and standard deviation of flow velocity at one point in space. Similarly, because of the spatially heterogeneous nature of turbulent flow, turbulence intensity estimated at a small spatial scale (1 cm^3) may be different from that estimated at a larger spatial scale (1 dm^3).

The turbulence of the flow in rivers may be an important factor influencing the activity costs of fish in these environments (Fausch 1993; McLaughlin and Noakes 1998). However, turbulence is not taken into account by either forced or spontaneous swimming models. The objectives of this study were (*i*) to determine the effect of turbulence on fish swimming costs, (*ii*) to compare the cost of swimming in turbulent flow to the costs predicted by forced and spontaneous swimming models, and (*iii*) to propose a new model to estimate the energetic cost of swimming in a turbulent flow.

Material and methods

We attained our objectives by performing 20 respirometry experiments during which we subjected individual fish to four types of turbulent conditions (a combination of two means and two standard deviations of the flow velocity). We performed five experiments per flow condition at a water temperature of 15 °C. Fish respiration rates obtained under the different turbulent conditions were compared with predictions made by forced and spontaneous swimming models (Boisclair and Tang 1993). This strategy was adopted because our experimental setup was not designed to provide and does not allow laminar flow or flow without turbulence. As such, we preferred to use, as a reference for comparisons, the 40 years of data on forced and spontaneous swimming available in the literature and used by Boisclair and Tang (1993) to develop general forced and spontaneous swimming models.

Fish

Juvenile Atlantic salmon (age-1+ *Salmon salar*; JAS) were selected for our study because their natural habitat encompasses gravel-bed rivers characterized by highly turbulent flows. The behaviour of JAS comprises so-called "sit-and-wait" periods in which JAS swim just above the substrate, often at the downstream edge of a rock, used as a protection against the turbulent flow. The rock preferentially used by a territorial JAS is referred to as its "home-rock". The sit-and-wait behaviour represents the largest part of the time budget of JAS (>80%; F. Burton and D. Boisclair, unpublished data). JAS also perform "attacks", which are feeding motions from the riverbed towards the water surface, or in the water column, in which they capture drifting invertebrates (Kalleberg 1958). During these motions, JAS experience rapid changes in the structure of flow. JAS were also used for our work because the abundance of wild Atlantic salmon is decreasing (Bardonnet and Baglinière 2000). This situation is alarming, particularly considering that these fish supported extensive and valuable commercial and recreational fisheries. It is expected that an improved assessment of the costs of habitat utilization for JAS would contribute to the development of models and management strategies of riverine environments better adapted to protect this species.

The Pisciculture de Tadoussac (operated by the Société de la Faune et des Parcs du Québec, Canada) provided the JAS used for our experiments. These were F_1 generation fish from the crossing of wild genitors that originated from the Sainte-Marguerite River (Saguenay Region, Québec, Canada). The juveniles were transferred to the Université de Montréal and kept in a 500-L Living Stream aquarium (model LSW 700; Frigid Units Inc., Toledo, Ohio) at 15 °C for a period of 1 month before beginning the experiments. This temperature was selected because it corresponded to the mean summer temperature of the Sainte-Marguerite River (Burton and Boisclair, unpublished data). The pH of the water was 7.8. Total hardness was 116 $mg \cdot L^{-1}$ $CaCO_3$, and water alkalinity was 83 $mg \cdot L^{-1}$ $CaCO_3$. The water was kept oxygen-saturated by airstones. Fish were fed daily with commercial food pellets (Corey Feed Mills Ltd., Fredericton, New Brunswick). The mean mass of the fish used for our respirometry experiments was 10.09 g wet (total number of fish used in our experiments (N) = 20, standard deviation (SD) = 0.33 g wet; mean total length (TL) = 10.8 cm, SD = 0.4 cm).

Experimental design

The respirometer consisted of a Plexiglas® box having a volume of 24 L (60 cm × 20 cm × 20 cm) with a lid that could be hermetically sealed. The respirometer was placed

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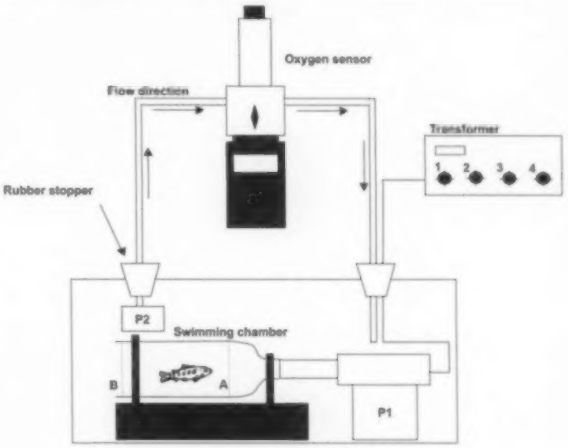
in a 500-L Living Stream aquarium to maintain a water temperature of 15 °C during the experiments. The respirometer contained two pumps and a bottle-shaped swimming chamber. The size of the respirometer was dictated by the size of the two pumps and that of the swimming chamber used. The pumps were inserted in the respirometer to insure that oxygen could not be introduced in the respirometer by the water flowing in the pumps. The size and the shape of the swimming chamber were selected to insure that fish could not avoid the flow and to minimize the influence of wall effects on our fish. Such wall effects may, at times, create vortices or more laminar flows near solid surfaces. Hence, flow structure closer to walls may be different from that in the center of a swimming chamber. Using a much smaller swimming chamber would have meant that fish would have been closer to the walls of the swimming chamber and more prone to wall effects difficult to describe or quantify. The narrow neck of the swimming chamber was connected to a pump (model 1750; Jacobs Canada Inc., Mississauga, Ont.) that generated the turbulent flow in the swimming chamber by recirculating water within the respirometer (Fig. 1). This pump is hereafter referred to as pump 1. Another pump (model 402; Powerhead, Montréal, Québec; hereafter referred to as pump 2) served two purposes. Before an experiment, pump 2 was used to create a water exchange between the respirometer and the aquarium and, hence, provide oxygenated water to the respirometer. During an experiment, pump 2 was used to transfer water from the respirometer to the oxygen meter. The swimming chamber contained two grids. The grids consisted of nylon mesh of 9 cm in diameter perforated with 2 mm × 2 mm holes. The grids were located in the "upstream" and "downstream" sections of the swimming chamber. The upstream grid was used to produce a spatially uniform, fine turbulence flow structure within the swimming chamber (Tritton 1988). The downstream grid was designed to force the fish to remain in the swimming chamber without interfering with the flow.

Turbulence in the swimming chamber was created by modulating the electric current that powered pump 1. Four components of the electric current were adjustable: (1) the maximal electric current that determines the maximal flow velocity, (2) the minimal electric current that determines the minimal flow velocity, (3) the frequency of pulsation between a reduction of the electric current to introduce a pulsation of the water flow, and (4) the duration of the reduction of the electric current to manipulate the duration of low- and high-speed flow conditions. Flow structures were quantified using an Acoustic Doppler Velocimeter (ADV; Sontek, San Diego, Calif.). The ADV allowed us to record the three orthogonal velocity vectors of the flow (streamwise, U; vertical, V; lateral, W) at a frequency of 25 Hz. The volume sampled by the ADV (0.25 cm^3) is located 5 cm away from its probe so that the perturbation of the measured flow by the probe is minimized. This volume (cylinder of 0.9 cm horizontally and a radius of 0.6 cm) was judged appropriate for our purposes because it resembled the product of the surface area of the cross section of the head and the length of the head of the fish used. The volume sampled by the ADV was therefore similar to the volume of the head of the fish used. The ADV permitted us to define the settings of the components of the electric current that could create four different flow conditions

Fig. 1. Schematic representation of the experimental setup used during the respirometry experiments performed to estimate the cost of swimming in a turbulent flow. A transformer modulated the electric current that powered a pump (P1), which created a turbulent flow in the swimming chamber against which a fish would swim. A second submerged pump (P2) continuously transferred water from the swimming chamber to the oxygen sensor to measure the oxygen uptake by a fish. The swimming chamber contained two grids. The "upstream" grid (A) was used to produce a spatially uniform fine turbulence flow structure within the swimming chamber, and the "downstream" grid (B) was designed to force the fish to remain in the swimming chamber.



determined by two mean streamwise flow velocities $\bar{u}$ (low flow condition = 18 $cm \cdot s^{-1}$; high flow condition = 23 $cm \cdot s^{-1}$) and two standard deviations of the streamwise flow velocity u_{SD} (low turbulence = 5 $cm \cdot s^{-1}$; high turbulence = 8 $cm \cdot s^{-1}$). The four experimental flow structures were selected for our experiments because they corresponded to flow conditions commonly used by JAS in the Sainte-Marguerite River (Guay et al. 2000; E.C. Enders and D. Boisclair, unpublished data). Fish activity costs were quantified by measuring the oxygen depletion over time with an oxygen meter (model 565 (Intab, Stenkullen, Sweden); ±0.005 mg $O_2 \cdot L^{-1}$).

Experimental procedure

Characteristics of flow structures

Turbulence was quantified at the beginning and end of the suite of experimental observations (five experiments) aimed at testing the effect of one of the four specific flow conditions on fish respiration rate. Turbulence was quantified in the absence of fish to avoid interference caused by fish on our recordings. For every flow condition, six velocity time series (three at the beginning and three at the end of a suite of experimental observations) were recorded for a period of 5 min. Between each velocity time series, the apparatus used to create the turbulent flow was completely shut down. This strategy was adopted to verify the repeatability and the stability of the flow structures created by our apparatus for given settings of the electric current that powered the pump.

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Respirometry

Respirometry experiments were performed using a single fish at a time. A fish was selected at random from our stock of experimental fish, kept separately, and not fed for 2 days before the experiment to avoid increased metabolic rates resulting from digestion (Brett and Groves 1979). Twenty-four hours before the beginning of an experiment, the fish was introduced into the swimming chamber to allow it to adapt to the experimental conditions. After this introduction, the respirometer was sealed without residual air bubbles. During this adaptation phase, pump 2 generated a water exchange between the respirometer and ambient water of the aquarium. At the beginning of the experiment, pump 2 was connected to the oxygen meter, preventing an external water supply, and pump 1 was started to create the turbulent flow structures in the swimming chamber. Oxygen concentration was measured at the beginning of the experiment, after which it was measured every 30 min for the duration of the experiment (6 h) for a total of 13 oxygen concentration measurements.

We monitored fish behaviour during each experiment to insure that they were continuously swimming. Every 10 min, an image of the position held by the fish within the swimming chamber was automatically registered with a Sony Webcam (Sony Electronics Inc., Oradell, N.J.). In addition, during the last 30 min of the experiment, the fish was continuously filmed by a video camera (WV-BL602; Panasonic Canada Inc., Lachine, Québec). Hence, our procedure presumes that if a fish is always in a swimming position in a series of images registered at 10-min intervals and if it swims continuously during the last 30 min of an experiment, it was continuously swimming during the 6 h of the experiment. Analysis of the images and of the films collected during our 20 experiments indicated that fish were always swimming in the central section of the swimming chamber. No fish settled at the bottom of the swimming chamber or was observed against the upstream or downstream grid of the swimming chamber. Consequently, we are proceeding with the assumption that during our experiments, fish were continuously swimming against the flow structures created by our apparatus.

An experiment always ended after 6 h. This 6-h period was chosen because performing longer (few hours but without provoking fatigue; see Discussion) rather than shorter experiments (few minutes) may allow oxygen depletion estimated during the respirometry experiments to include the repayment of an oxygen debt incurred by the recourse by fish to anaerobic metabolism. No observation was made under 7.6 mg $O_2 \cdot L^{-1}$ to minimize the influence of low oxygen concentration on the fish behaviour (Beamish 1978). At the end of an experiment, the fish was removed from the respirometer, anaesthetized (clove oil; 0.6 mg$\cdot L^{-1}$), weighed (g wet), and measured (TL, cm). The biological oxygen demand (BOD) was determined within 6 h of an experiment using the same procedure but without fish.

Computations

We estimated the cost of swimming against a turbulent flow in three steps. Firstly, we estimated the total metabolic rate of fish (C_R, mg $O_2 \cdot h^{-1}$) as

$$(1) \quad C_R = \Delta O_2 / \Delta t \cdot V_W - \text{BOD}$$

where ΔO_2 is the difference in oxygen concentration between two consecutive oxygen concentration measurements (mg $O_2 \cdot L^{-1}$), Δt is the time interval of 0.5 h between two consecutive oxygen concentration measurements, V_W (22.6 L) is the volume of water in the respirometer excluding the volume of our pumps and swimming chamber, and BOD is the biological oxygen demand by micro-organisms in the water (mg $O_2 \cdot h^{-1}$). BOD ranged from 0.001 to 0.004 mg $O_2 \cdot h^{-1}$. Because we measured oxygen concentration within the swimming chamber at 30-min intervals over 6 h, we obtained 12 C_R values per experiment. Secondly, we calculated the mean (further referred to as C_M, mg $O_2 \cdot h^{-1}$) and the standard deviation of the C_R values obtained for each experiment. Thirdly, the cost of swimming against a turbulent flow (C_A, mg $O_2 \cdot h^{-1}$) was estimated as

$$(2) \quad C_A = C_M - \text{SMR}$$

where SMR is the standard metabolic rate of a fish (mg $O_2 \cdot h^{-1}$). The standard metabolic rate was determined by a model that we developed using data from Brett and Glass (1973) on the standard metabolism of juvenile sockeye salmon (*Oncorhynchus nerka*) weighing 4–10 g and held at a water temperature of 15 °C

$$(3) \quad \text{SMR} = 0.227M^{0.653} \ (n = 5;\ r^2 = 0.86;\ p < 0.05)$$

where M is the body mass of the fish (g wet). SMR values were obtained by extrapolating the relationship between oxygen consumption and mean flow velocity from forced swimming experiments to zero velocity. According to eq. 3, SMR for the fish used in our experiments ranged from 1.00 to 1.07 mg $O_2 \cdot h^{-1}$.

Statistical analysis

The repeatability of each of the four experimental flow structures created by our apparatus was tested using one-way analysis of variance (ANOVA). Such ANOVA was performed to compare the mean streamwise flow velocities during the three times series recorded before a suite of experimental observations. The analysis was also done for the three velocity time series obtained after a suite of experimental observations. The stability of the turbulent flow structures was tested using a one-way ANOVA comparing the mean flow velocities before with those after a suite of experimental observations. During this analysis, the three velocity time series obtained before or after a suite of experimental observations were used as replicates. The repeatability and the stability of the standard deviations of the flow velocities were tested using the same approach with Levene's test of the equality of variances. This test was selected because it has been argued to be more robust and not dependent on the assumption of normality compared with, for example, the Bartlett's test of equality of variances (Scherrer 1984).

We confirmed the periodicity of the pulsating flow using a power spectrum analysis (Lapointe et al. 1996). Every 5-min velocity time series measured with the ADV were filtered using a Gausian filter. The filtered time series was decomposed in frequencies using a Fourier transformation (Legendre and Legendre 1998). The power spectrum analysis measures the variance contributions from different frequencies within the

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velocity time series. The total variance of the time series is presented as the area under a relationship between the variance associated to a frequency and the frequency (referred to as a power spectrum). Spikes in the power spectrum indicate a periodicity with the corresponding frequency.

Low- and high-speed flow events within the velocity time series were identified using conditional analysis. These events were defined as velocity fluctuations above or below the mean streamwise velocity that lasted more than 0.75 s (Lu and Willmarth 1973).

Swimming costs were compared among the four different flow structures with a two-way ANOVA using mean flow velocity and standard deviation of flow velocity as classification variables. The five replicates of swimming costs for each flow structure allowed us to test the statistical significance of the interaction term of this analysis (mean flow velocity × standard deviation of flow velocity).

The activity costs that we estimated while fish were swimming against a turbulent flow were compared with predictions made by the forced and the spontaneous swimming models developed by Boisclair and Tang (1993). Both models were inputted with the mass of the fish and the mean flow velocity used during our experiments. Activity costs predicted by the forced or spontaneous models were compared with observed activity costs using model II regression analysis. The null hypothesis in this analysis was that there is no statistically significant difference between predicted and observed activity costs. The slope of the regression line was tested against an expected value of unity, and the intercept was tested against an expected value of zero. The statistical significance and the 95% confidence intervals of the slope and the intercept of the major axis estimates were tested with 999 permutations (Legendre and Legendre 1998).

Results

Characteristics of flow structures

The means and the standard deviations of the streamwise flow velocities recorded were consistent with the targeted values (Table 1). The mean streamwise flow velocities ranged from 18.02 to 18.32 cm·s^{-1} for the low flow condition (target = 18 cm·s^{-1}) and from 23.02 to 23.09 cm·s^{-1} for the high flow condition (target = 23 cm·s^{-1}). The standard deviation of the streamwise flow velocity under the low turbulent conditions ranged from 5.06 to 5.16 cm·s^{-1}. Corresponding values under the high turbulent conditions ranged from 7.92 to 8.27 cm·s^{-1} (Table 1). The mean vertical flow velocities ranged from –0.70 to 0.44 cm·s^{-1} for low flow velocities and from –0.10 to 0.12 cm·s^{-1} for high flow velocities. The standard deviation of the vertical flow velocity ranged from 4.79 to 5.04 cm·s^{-1} under the low turbulent conditions and from 6.93 to 7.64 cm·s^{-1} under high turbulent conditions. Corresponding values for the mean lateral flow velocities ranged from –0.45 to 0.49 cm·s^{-1} for low flow and from 0.20 to 0.32 cm·s^{-1} for high flow conditions. The standard deviation of the velocities under the lateral flow ranged from 5.41 to 5.62 cm·s^{-1} under low turbulence and from 7.50 to 7.71 cm·s^{-1} under high turbulence conditions.

For any given flow condition, the mean streamwise flow velocity $\bar{u}$ and the standard deviation of streamwise flow velocity u_{SD} did not vary significantly among the three recordings performed before (variation = 0.1–1.8%) or after (variation = 0.1–1.8%) a suite of experimental observations (Repeatability test: $\bar{u}$, $0.656 < p < 0.998$; u_{SD}, $0.196 < p < 0.989$). Similarly, for any given flow condition, the mean streamwise flow velocity $\bar{u}$ and the standard deviation of streamwise flow velocity u_{SD} obtained before a suite of experimental observations did not vary significantly (variation = 0.0–2.0%) from values estimated after a suite of experimental observations (Stability tests: $\bar{u}$, $0.917 < p < 0.998$; u_{SD}, $0.464 < p < 1.000$). These results suggest that the flow structures created by our apparatus were repeatable and stable.

The spike at 0.17 Hz in the power spectrum analysis confirmed the presence of a dominant period of 6 s within the velocity time series (Fig. 2). However, the power spectra also showed the occurrence of a variety of frequencies, signifying the presence of a fully developed turbulent flow. The examination of the velocity time series allowed us to identify from two to five low-speed flow events/min and five high-speed flow events/min. The mean duration of the flow events was 1.0 s. The standard deviation of the duration of the flow events ranged from 0.20 to 0.29 s (Table 2).

Swimming costs

Swimming costs varied threefold among our experiments, ranging from 1.46 ($\bar{u}$ = 18 cm·s^{-1}; u_{SD} = 5 cm·s^{-1}) to 4.42 mg O_2·h^{-1} ($\bar{u}$ = 23 cm·s^{-1}; u_{SD} = 8 cm·s^{-1}; Fig. 3). These values corresponded to a factor ranging from 1.4 to 4.3 times SMR. Swimming costs tended to increase with mean flow velocity ($p < 0.01$) and with the standard deviation of the flow velocity ($p < 0.01$). The interaction between the mean and the standard deviation of flow velocity was also significant ($p < 0.01$), indicating that an increase of standard deviation of flow velocity did not have the same effect for the low and high flow conditions. An increase of the standard deviation of flow velocity from 5 to 8 cm·s^{-1} increased activity metabolic rates by factor of 1.3 at a low flow conditions. This factor was 1.6 at high flow conditions (Table 3).

Comparison between observed swimming costs and predictions by forced and spontaneous swimming models

Predictions of activity costs obtained using the forced swimming model tended to underestimate observed activity costs. At low flow conditions, the forced swimming model underestimated the observed cost of swimming of JAS subjected to turbulent flows by a factor ranging from 1.9 (u_{SD} = 5 cm·s^{-1}) to 2.4 (u_{SD} = 8 cm·s^{-1}). Corresponding values at high flow conditions ranged from 2.6 (u_{SD} = 5 cm·s^{-1}) to 4.2 (u_{SD} = 8 cm·s^{-1}; Table 4). The 95% confidence interval of the intercept of the regression model between observed and predicted respiration rates ranged from 0.55 to 0.74. This intercept was statistically different from zero (p = 0.001). The 95% confidence intervals of the slope of the regression model between observed and predicted respiration rates ranged from 0.07 to 0.13. This slope was significantly different from unity (p = 0.001).

Activity costs predicted by the spontaneous swimming model of Boisclair and Tang (1993) always overestimated swimming costs in turbulent flows (Fig. 4). At the low flow velocity, the spontaneous swimming model overestimated the

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Table 1. Ranges of the mean flow velocity and the standard deviation of the flow velocity ($cm \cdot s^{-1}$) during the six 5-min velocity time series. Ranges of minimum and maximum flow velocity ($cm \cdot s^{-1}$) for the streamwise U (u_{min}, u_{max}), vertical V (v_{min}, v_{max}), and lateral W (w_{min}, w_{max}) velocity vectors in the four different flow conditions and the ranges of their standard deviations (u_{SD}, v_{SD}, w_{SD}, respectively) are also presented.

Velocity vector	Low velocity – low turbulence	Low velocity – high turbulence	High velocity – low turbulence	High velocity – high turbulence
Range $\bar{u}$	18.02–18.18	18.26–18.32	23.02–23.08	23.02–23.09
Range u_{SD}	5.06–5.16	8.16–8.27	5.07–5.15	7.92–8.08
u_{min}	3.11–4.63	0.27–1.64	3.47–5.64	0.35–0.90
u_{max}	34.21–35.36	36.34–38.94	34.47–36.88	42.24–44.85
Range $\bar{v}$	–0.70–0.34	–0.42–0.44	–0.10–0.10	–0.10–0.12
Range v_{SD}	4.79–4.94	6.93–7.05	4.81–5.04	7.14–7.64
v_{min}	–23.02–(–18.74)	–25.83–(–22.04)	–29.77–(–27.35)	–31.41–(–28.39)
v_{max}	20.61–22.95	21.52–24.26	27.84–31.45	29.20–30.65
Range $\bar{w}$	0.15–0.19	–0.45–0.49	–0.20–0.10	0.30–0.32
Range w_{SD}	5.41–5.57	7.50–7.69	5.42–5.62	7.53–7.71
w_{min}	–26.27–(–20.38)	–27.49–(–22.31)	–21.71–(–35.37)	–24.95–(–30.61)
w_{max}	22.64–23.82	25.08–28.23	29.62–33.31	29.04–35.74

Fig. 2. Relationship between the spectral density and the frequency of the streamwise velocity vector U of the time series for four different flow conditions (two mean water velocities $\bar{u}$ of 18 and 23 $cm \cdot s^{-1}$ and two standard deviations u_{SD} of 5 and 8 $cm \cdot s^{-1}$).

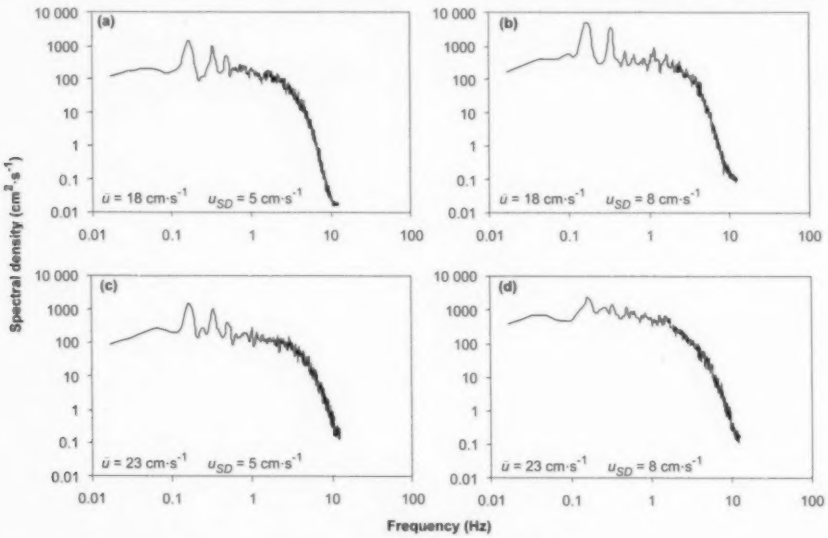

Table 2. Number and duration of low- and high-speed flow events for each of the four turbulent conditions.

	Low velocity – low turbulence	Low velocity – high turbulence	High velocity – low turbulence	High velocity – high turbulence
Number of low-speed flow events/min	2	3	2	5
Number of high-speed flow events/min	5	5	5	5
Mean duration (s)	1	1	1	1

swimming costs in a turbulent flow by a factor ranging from 6.6 (u_{SD} = 5 $cm \cdot s^{-1}$) to 5.0 (u_{SD} = 8 $cm \cdot s^{-1}$). The overestimation of respiration rates predicted by the spontaneous model was decreased to factors ranging from 4.5 (u_{SD} = 5 $cm \cdot s^{-1}$) to 2.8 (u_{SD} = 8 $cm \cdot s^{-1}$) at high flow conditions. The 95% confidence intervals of the intercept associated with the regression model between observed and predicted oxygen consumption rates ranged from 7.11 to 9.15. The intercept of

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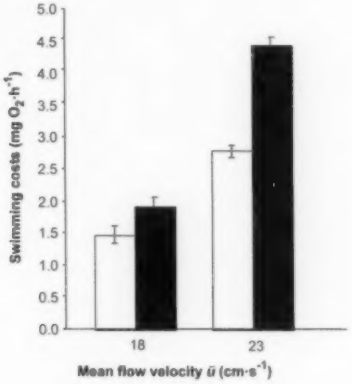
Fig. 3. Swimming costs of juvenile Atlantic salmon (*Salmo salar*) under four turbulent conditions defined by the mean flow velocity ($\bar{u}$) and the standard deviation of flow velocity (u_{SD}). Low turbulence conditions (u_{SD} of 5 cm·s^{-1}) are represented by open bars and high turbulent conditions (u_{SD} of 8 cm·s^{-1}) are represented by solid bars. Vertical lines represent 95% confidence intervals.



this regression model was significantly different from zero ($p = 0.001$). The 95% confidence interval of the slope of the relationship between observed and predicted activity costs ranged from 0.73 to 1.44. This slope was not significantly different from the expected value of 1 ($p > 0.05$).

Discussion

Our analyses indicate that the swimming costs of JAS in turbulent flow may significantly increase as mean flow velocity and standard deviation of the flow velocity increase. In our experiments, swimming costs increased by an average factor of 1.5 as mean flow velocity increased from 18 to 23 cm·s^{-1}. The effect of mean flow velocity on fish respiration rates is not surprising as it is imbedded in all swimming cost models currently available (Beamish 1978; Boisclair and Tang 1993; Tang et al. 2000). We also found that swimming costs for a given mean flow velocity may increase with the standard deviation of the flow velocity. In our study, fish respiration rates increased, on average, by a factor of 2.1, as the standard deviation of the flow velocity increased from 5 to 8 cm·s^{-1}. Our analyses also showed that the effect of increasing the intensity of the turbulence of flow may increase as mean flow velocity increases. As the standard deviation of the flow velocity increased from 5 to 8 cm·s^{-1}, swimming costs of JAS increased by a factor of 1.3 at a mean flow velocity of 18 cm·s^{-1} and by a factor of 1.6 at a mean flow velocity of 23 cm·s^{-1}.

Our work may be taken as an indication that not only mean flow velocity, but also standard deviation of flow may be required to adequately estimate the cost of swimming under turbulent conditions. However, our data do not really allow us to fully evaluate the ultimate cause of the variation of fish respiration rates among our treatments. Although our methods focus mostly on the mean and the standard deviation of flow velocity, any other characteristic such as the number and the intensity of the flow events may affect the metabolic rates of fish. In our study, experimental treatments did not only vary in terms of mean and standard deviation of velocity, but also in terms of the number of events per minute (particularly low-speed flow events). This is expected because the descriptors of turbulence are expected to be correlated: high turbulence is expected to have more flow events per unit of time and a higher SD flow/mean flow than low turbulence; high velocity is expected to have faster flow and more events per unit of time than low velocity. In our study, among-experiment variability in flow structure was expressed by more low-speed events in high turbulence conditions (3–5/min) than in low turbulence conditions (2/min; high-speed events were always 5/min). Similarly, more events occurred under high-speed conditions (5 low-speed events/min) than under low-speed conditions (3 low-speed conditions/min). Because the descriptors of flow are interrelated, it is presently impossible with the few data that we have to assess the relative effect of mean flow, standard deviation of flow velocity, and the number of flow events (and, potentially, the magnitude of flow events or the type of flow event, high or low) on fish respiration. Our present contribution is limited to providing estimates of the effect that turbulence may have on fish respiration, notwithstanding its ultimate cause.

The applicability of our results to field situations depends on the ability of our experimental design to reflect natural conditions found in rivers and streams and on the validity of the assumptions that we used to estimate fish swimming costs. Activity metabolism is generally estimated using forced swimming experiments seeking to minimize heterogeneity of flow velocity and direction (Brett 1965; Beamish 1978) or using spontaneous activity experiments in absence of flow (Boisclair and Tang 1993; Krohn and Boisclair 1994; Tang and Boisclair 1995). Because rivers are characterized by temporally heterogeneous flow, we expected that using an experimental design that does not only allow flow to be present but to be varied may better represent natural flow conditions faced by the fish. Both mean and standard deviation of the flow velocity used during our experiments were chosen to represent a subset of the natural conditions encountered by JAS. The two experimental mean flow velocities ($\bar{u}$ = 18 and 23 cm·s^{-1}) are within the range of focal point and microhabitat velocities used by JAS (DeGraaf and Bain 1986; Morantz et al. 1987; Guay et al. 2000). The experimental standard deviations of 5 and 8 cm·s^{-1} were adopted following field observations of habitat selected by JAS in the Sainte-Marguerite River (Enders and Boisclair, unpublished data). Natural flow conditions comprise realistic flow structures such as temporal successions of fast- and slow-moving flow events extending over the whole water column (Kirkbride and Ferguson 1995; Ferguson et al. 1996). In gravel-bed rivers, flow events lasting from 0.5 to 5 s have been shown to occur at 5- to 30-s intervals (Roy et al. 1999). Consequently, we controlled the electric current powering the pump that created a pulsating flow such that our apparatus produced slow flow events of a mean duration of 1 s at 6-s intervals. Hence, we performed our experiments under combinations of mean flow velocity, standard deviation of the flow velocity, duration of flow events, and interval between flow events that are within the range found under natural conditions.

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Table 3. Number of respirometry experiments (N) per flow condition (combinations of mean flow velocity $\bar{u}$ and standard deviation of the flow velocity (u_{SD})), mean fish mass (M), costs of swimming (C_A) in the corresponding turbulent flow condition, and standard deviation (SD) of C_A among the five experiments.

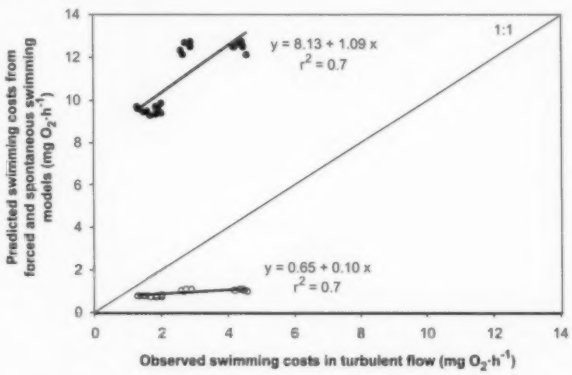
N	$\bar{u}$ (cm·s^{-1})	u_{SD} (cm·s^{-1})	M (g)	C_A (mg O_2·h^{-1})	SD of C_A (mg O_2·h^{-1})
5	18	5	10.01	1.46	0.17
5	18	8	10.15	1.91	0.08
5	23	5	10.09	2.77	0.12
5	23	8	10.13	4.42	0.15

Table 4. Comparisons between the observed activity metabolic rate for given combinations of mean flow velocity ($\bar{u}$) and standard deviation of the flow velocity (u_{SD}) and the predictions of forced and spontaneous swimming model of Boisclair and Tang (1993) implemented with mean flow velocity.

$\bar{u}$ (cm·s^{-1})	u_{SD} (cm·s^{-1})	Factor 1	Factor 2
18	5	1.9	6.6
18	8	2.4	5.0
23	5	2.6	4.5
23	8	4.2	2.8

Note: Factor 1 represents the factor by which the predictions of the forced swimming model underestimated observed activity metabolic rates. Factor 2 represents the factor by which spontaneous swimming model overestimated observed activity metabolic rate.

Fig. 4. Comparison between the observed swimming costs of juvenile Atlantic salmon (*Salmo salar*) of 10 g under four different turbulent conditions (two mean flow velocities $\bar{u}$ of 18 and 23 cm·s^{-1} and two standard deviations u_{SD} of 5 and 8 cm·s^{-1}) and the swimming costs predicted by the forced (open circles) and the spontaneous (solid circles) swimming models of Boisclair and Tang (1993).



However, our results do not cover the complete range of conditions that may be encountered in natural environments. Furthermore, flow characteristics other than those that we studied may affect fish swimming costs. For instance, Webb (1993*a*) described that "ground effects" created by solid structures, such as the walls of our swimming chamber, increase lift, reduce drag, and therefore decrease swimming costs. Fish from our experiments may have been subjected to such effects. In view of our objectives, the presence of ground effects may not affect the relevance of our results to field situations. In their natural habitat, JAS spend most of their time swimming just above the substrate (sit-and-wait behaviour). However, the difference between the ground effects perceived by fish in our swimming chamber and those experienced by fish under natural conditions and the effect of such a difference on the applicability of our results to field situations represents a more important issue for which we have no immediate solution. Similarly, because we measured flow velocity only in one central point of the swimming chamber, we cannot describe the form and size of the vortices that may have been present in our swimming chamber. Theoretically, the upstream grid introduced in the swimming chamber should prevent the occurrence of large vortices or recirculation zones that would decrease the energy expenditure of fish (Tritton 1988). Although the existence of such recirculation zones in our swimming chamber should be assessed to better interpret our results, two lines of evidence suggest that JAS were not subjected to a significant effect of vortex. First, negative streamwise flow velocities were not observed in our swimming chamber. This indicates that during our experiments, JAS were not submitted to a counter-streamwise flow. Second, the vertical (V) and lateral (W) flow velocity components were highly variable (range = –31.41 to 31.45 cm·s^{-1}) and directionally unstable (from negative to positive values). This suggests that fish were not subjected to directionally stable conditions that characterize recirculation zones (Vogel 1994). Consequently, the swimming costs estimated may not be representative of those incurred by JAS when they hold position on the downstream end of a rock (where vortices and recirculation zones are expected to occur). However, the respiration rates obtained may adequately represent the cost of swimming against a turbulent flow (with similar mean and standard deviation of flow velocity) while JAS perform the attack phase of their feeding motions to capture prey items.

During our experiments, JAS were continuously swimming over a 6-h period. However, in their natural environment, JAS may swim against a turbulent flow only during shorter time periods than those used in our experiments (attacks directed towards invertebrates that drift in the flow, aggressive interactions, habitat exploration). Although we recognize that the duration of our experiments may have been demanding to the fish, within-experiment variation in oxygen consumption rates during 30 min (C_R) ranged from 3.8% to 11.6%. Furthermore, we found no relationship between C_R and time since the beginning of an experiment ($0.01 < r^2 < 0.134$; $0.24 < p < 1$). Hence, our experimental

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conditions did not appear to cause any functionally or statistically significant fatigue to the fish used.

The method used to estimate fish swimming costs is based on the assumption that the standard metabolic rate (SMR) of Atlantic salmon is adequately represented by that of sockeye salmon of similar sizes (Brett and Glass 1973). The use physiological models developed for one species to predict bioenergetic attributes of another species may produce potentially misleading estimates (Ney 1993). Our use of the SMR data of sockeye salmon for Atlantic salmon was motivated by the absence of SMR data specific to Atlantic salmon, by the availability of a large data set for sockeye salmon, and by the taxonomic (both salmonids), morphological (body mass–length relation), physiological (preferred water temperature), and ecological (juvenile stages in riverine freshwater) similarities between both species. However, it may be hypothesized that SMR for similar-sized fish held at a same water temperature vary among different salmonid species. To our knowledge, the only data that may allow us to test this hypothesis are the SMR data of Job (1955) for brook char (*Salvelinus fontinalis*) ranging from 5 to 2000 g at 15 °C. Job (1955) estimated SMR as the lowest hourly respiration rates of fish held in a rectangular respirometer during 24 h. Applying the SMR model of brook trout to the fish size used in our experiments, we obtained SMR values ranging from 1.02 to1.12 mg $O_2 \cdot h^{-1}$. Corresponding values obtained with the model based on data collected for sockeye salmon, and used during our computations, ranged from 0.99 to 1.07 mg $O_2 \cdot h^{-1}$. The 2.4–4.5% difference between SMR obtained for two different species of salmonids suggests that the use of the SMR model of sockeye salmon to predict the SMR of Atlantic salmon may have a minor effect on our estimates of swimming costs.

Forced and spontaneous swimming models are presently the most commonly used models to estimate the swimming costs of fish. Comparisons between predictions made by these models and our estimates of the cost of swimming under turbulent flow allowed us to assess the effect of turbulence of swimming energetics. However, it is useful to compare models that are subjected to similar assumptions. Three basic assumptions are shared by all swimming cost models. Firstly, all types of models assume that experimental conditions allow fish to swim in a manner that may mimic their swimming in the field. Experimental approaches differ with respect to the probability that this assumption may be true. For instance, during forced swimming experiments, fish are forced to swim against a flow of constant velocity and direction (no acceleration and no turns are allowed). Such flow is rarely present in the field. Therefore, fish may rarely swim at a constant speed and direction, whether against a flow or in a body of water without any flow. In turbulent swimming experiments, fish are forced to swim against a turbulent flow, which does exist in the field. During spontaneous swimming experiments, fish control their swimming speed. They are also allowed to freely perform accelerations and turns. As such, spontaneous swimming models may be expected to be the closest to natural conditions for fish living in habitats that have no significant flow (lakes, ponds, etc). Secondly, all models assume that within the range of the duration of the experiments performed, the length of an experiment (h) has no effect on the validity of the respiration rates obtained (i.e., respiration rates/h estimated over 30 s is identical to respiration rates/h estimated over 6 h). Forced and turbulent swimming experiments are particularly susceptible to this assumption because experiments often require that fish swim continuously for hours, which may not correspond to the natural behaviour of most fish species. Both types of approaches assume that if fish continue to swim for the complete duration of an experiment and if respiration rates do not significantly increase or decrease through time, then fish are not fatigued and their respiration rates adequately represent swimming costs under the experimental conditions. As such, when developing swimming cost models, combinations of swimming intensity and duration of the experiments are selected to avoid fatigue. Spontaneous swimming experiments are not affected by this assumption because fish are free to swim or to remain immobile. Thirdly, all models assume that swimming costs are adequately estimated by measuring oxygen consumption by fish. This assumption also presumes that the energy required to swim comes mostly from the aerobic metabolism. If anaerobic metabolism contributes to fish swimming costs, then the potential exists for oxygen consumption rates to underestimate actual swimming costs. However, the absolute or relative contribution of aerobic and anaerobic metabolism is difficult to establish and is rarely estimated. Yet, anaerobic metabolism could theoretically interfere with estimates of fish swimming costs obtained by measuring oxygen consumption by fish under forced, turbulent, or spontaneous swimming experiments. Indeed, even under spontaneous swimming experiments, fish may occasionally perform intense accelerations that may require anaerobic metabolism. The interference caused by anaerobic metabolism is circumvented by modulating the experimental flow velocities and the duration of the experiments to minimize the expression of anaerobic metabolism. It is expected that avoiding extreme velocities may minimize the use by fish of anaerobic metabolism. Furthermore, performing longer (few hours but without provoking fatigue) rather than shorter experiments (few minutes) may allow oxygen depletion estimated during the respirometry experiments to include the repayment of an oxygen debt incurred by the recourse to anaerobic metabolism. Hence, the three approaches to estimate or model fish swimming costs rest on the same basic assumptions.

Generally, the three approaches employ the same strategy (selection of experimental flow velocities, assessment of trends of fish respiration rates during experiments, selection of the duration of experiments) to measure, avoid, and minimize the effects of these assumptions. Another element common to all three approaches is that fish respiration rates are modeled using fish mass, flow velocity, or fish swimming speed. This facilitates the comparison among models, although it may be necessary for fish living in turbulent flows, as illustrated by our work, to add descriptors of the complexity of flow (e.g., standard deviation of flow) to this list of independent variables. Providing evidence that the inclusion of such descriptors in swimming cost models for fish living under turbulent conditions may not only be necessary, but also achievable, may constitute the most important contribution of our work. It is our contention that the comparisons that we performed among the different models is justified not only from a fundamental perspective, but also from a func-

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tional perspective. Although it may be conceptually obvious that using forced swimming models to estimate the cost of swimming for fish swimming against a turbulent flow may be incorrect, a number of recent studies used this approach because of the lack of quantitative information about the effect that turbulence may have on fish swimming costs. The comparisons that we performed among swimming models allow users of such models to readily assess the functional and quantitative consequences of our work on estimates produced by the most commonly used models.

The swimming costs estimated under our experimental conditions were 1.9- to 4.2-fold larger than those predicted using a forced swimming model and 4.2- to 6.6-fold smaller than those predicted by a spontaneous swimming model. The higher respiration rates estimated under turbulent conditions relative to predictions made by forced swimming conditions are consistent with the suggestion of Webb (1982) and Boisclair and Tang (1993) that unsteady swimming (including changes in speed and direction) is more energetically costly than steady swimming (no changes in speed and direction). Changes in swimming speed and direction that must be performed under turbulent conditions may be expected to cause a substantial increase in the energy costs compared with steady swimming at the same average speed. Adjustments undertaken by fish with their fins to maintain their position in the water column are also expected to increase activity costs (Weatherley et al. 1982; Gauthier 1998; McLaughlin and Noakes 1998). The extensive use of fins provides stability but also increases drag (Webb 1993*b*), and as illustrated by our work, it increases energy expenditure at a same mean flow velocity. McLaughlin and Noakes (1998) noted a temporal variability in the tail beat frequency and amplitude of young-of-the-year brook trout observed in a natural stream. They suggested that these adjustments corresponded to the fluctuations of the flow velocity, which may increase the energetic costs for swimming against a turbulent flow. Our results are consistent with their suggestion.

Activity costs predicted by the forced swimming model that we used are expected to increase with swimming speed raised to a power of 1.21 (Boisclair and Tang 1993). An exponent greater than one suggests a relatively higher increase of activity cost with a given increase of swimming speed. Therefore, it may be hypothesized that the estimation of activity costs with instantaneous flow velocities instead of the mean flow velocity would improve the accuracy of the predictions made by the forced swimming model (e.g., peaks in flow velocities could lead to an important increase of the activity costs estimated using a model in which velocity has an exponent of 1.21). We tested this hypothesis by estimating the oxygen consumption rates predicted by the forced swimming model using flow velocity data recorded at 25 Hz (Table 5). Our results indicated that the use of instantaneous flow velocity, instead of the mean flow velocity, increased activity costs predicted by the forced swimming model by 2–6%. This analysis confirms that the use of forced swimming models in bioenergetic modeling of riverine fish species may underestimate actual cost of swimming in turbulent flow even when these models are implemented with instantaneous measures of flow velocity.

Our data suggest that the cost of swimming in a turbulent flow may be higher than predicted by forced swimming models but lower than expected when using spontaneous swimming models. In our study, the difference between actual swimming costs and those predicted by the forced swimming model increased with the mean and the standard deviation of flow. Furthermore, the difference between actual swimming costs and those predicted by the spontaneous swimming model decreased with the mean and the standard deviation of flow. Because our laboratory experiments simulated flow conditions from the lower part of the turbulence spectrum that may be observed under natural environments, we anticipate that the difference between actual swimming costs observed in our study and those predicted by the forced swimming model may be much lower than those that could be found in more extreme turbulent conditions. Similarly, we expect that the difference between actual swimming costs observed in our study and those predicted by the spontaneous swimming model may be higher than those that could be found in more extreme turbulent conditions.

Table 5. Comparisons between the cost of swimming (C_A) predicted by the forced swimming model of Boisclair and Tang (1993) implemented with the mean flow velocity ($\bar{u}$; $u_{SD} = 0$) and predictions of this model implemented with instantaneous flow velocities recorded at 25 Hz (u_{SD} = 5 or 8 cm·s^{-1}).

$\bar{u}$ (cm·s^{-1})	u_{SD} (cm·s^{-1})	C_A (mg O_2·h^{-1})	Factor A
18	0	0.77	—
18	5	0.79	1.03
18	8	0.82	1.06
23	0	1.04	—
23	5	1.06	1.02
23	8	1.07	1.03

Note: Factor A represents the factor by which the predictions increased because of the use of the instantaneous instead of the mean flow velocities.

The major difference between the movements performed by fish during spontaneous swimming experiments and those observed under the turbulent conditions that we used do not appear to reside in the standard deviation of fish swimming speed (or flow velocity) but in the intensity of the changes in direction. The variance of speed estimated during spontaneous swimming experiments generally range from 3.7 to 109 cm^2·s^{-2} (Tang and Boisclair 1995; Tang et al. 2000). These values correspond to standard deviations of 1.9 to 10.5 cm·s^{-1}. However, during spontaneous swimming experiments, fish perform turns ranging from 30.9 to 63.5° (Tang and Boisclair 1995). Such turns were not performed under the experimental conditions that we used. Hence, for a given swimming speed, lowest costs may be predicted by a forced swimming model (low standard deviation of the flow velocity and small angles of turns), intermediate costs may be predicted by a turbulent model developed under conditions similar to those used in our experiments (turbulent flow with intermediate levels of standard deviation of the flow velocity, e.g., 5–8 cm·s^{-1}, and small angles of turns), and the highest costs may be predicted with spontaneous models (high standard deviation of flow velocity and more pronounced angles of turns). This situation may indicate that for a given mean flow velocity or swimming speed, forced, turbulent, and spontaneous swimming data obtained for increasing standard deviation of flow velocities or swimming speeds and increasing angles of turns may form a continuum of increasing

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swimming costs. In the context of estimating the activity costs of JAS in the field, we speculate that such ranking may mean that the forced swimming model may be adequate to estimate the cost of swimming for fish facing flows of minimized heterogeneity (e.g., sit-and-wait position of fish near the substrate), that the turbulent swimming model may be adequate for fish inhabiting turbulent flow conditions, and that the spontaneous swimming model may be adequate for fish in more stringent conditions (complex swimming motions, high turbulence). Estimation of the activity costs of fish in turbulent flows may therefore require more than one model.

Our results suggest that bioenergetic models aimed at estimating the costs of habitat use by fish living in turbulent environments may require a description of the behaviour of the fish, estimates of the mean and the standard deviation of the flow, and respiration models in which the effects of the mean and the standard deviation of flow velocity are explicitly represented. Such an approach should be extended to studies using video observations (Trudel and Boisclair 1996; Aubin-Horth et al. 1999), radio tracking (Bourke et al. 1996; Ovidio 1999), and physiological telemetry (electromyograms; Korsmeyer et al. 1997; Dewar et al. 1999) in turbulent environments. We anticipate that models using the mean and the standard deviation of flow velocity may provide estimates of the costs of habitat utilization by fish living in rivers that are more accurate than commonly used forced swimming models. As such, our study suggests that the use of models more adequately representing the cost of swimming against a turbulent flow may strongly affect estimates of the cost of swimming and the expected balance of the benefits and costs of habitat utilization in turbulent environments.

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Physical forcing and the dynamics of the pelagic ecosystem in the eastern tropical Pacific: simulations with ENSO-scale and global-warming climate drivers

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Abstract: We used a model of the pelagic ecosystem in the eastern tropical Pacific Ocean to explore how climate variation at El Niño – Southern Oscillation (ENSO) scales might affect animals at middle and upper trophic levels. We developed two physical-forcing scenarios: (1) physical effects on phytoplankton biomass and (2) simultaneous physical effects on phytoplankton biomass and predator recruitment. We simulated the effects of climate-anomaly pulses, climate cycles, and global warming. Pulses caused oscillations to propagate through the ecosystem; cycles affected the shapes of these oscillations; and warming caused trends. We concluded that biomass trajectories of single populations at middle and upper trophic levels cannot be used to detect bottom-up effects, that direct physical effects on predator recruitment can be the dominant source of interannual variability in pelagic ecosystems, that such direct effects may dampen top-down control by fisheries, and that predictions about the effects of climate change may be misleading if fishing mortality is not considered. Predictions from ecosystem models are sensitive to the relative strengths of indirect and direct physical effects on middle and upper trophic levels.

Résumé : Un modèle de l'écosystème pélagique du Pacifique oriental tropical nous a permis d'explorer comment des variations à l'échelle d'El Niño et de l'oscillation australe (ENSO) peuvent affecter les animaux des niveaux trophiques moyens et supérieurs. Nous avons imaginé deux scénarios de forçage physique : (1) les effets physiques sur la biomasse du phytoplancton et (2) les effets physiques simultanés sur la biomasse du phytoplancton et le recrutement des prédateurs. Nous avons simulé les effets des pulsations des anomalies climatique, de cycles climatiques et du réchauffement global. Les pulsations engendrent des oscillations qui se propagent dans l'écosystème, les cycles modifient la forme des oscillations et le réchauffement global engendre des tendances. Nos conclusions sont les suivantes : les trajectoires de la biomasse de populations isolées des niveaux trophiques moyens ou supérieurs ne peuvent servir à déceler les effets ascendants; les effets physiques qui affectent directement le recrutement des prédateurs peuvent être la source principale de la variation inter-annuelle dans les écosystèmes pélagiques; de tels effets directs peuvent tamponner le contrôle descendant exercé par la pêche commerciale; les prédictions sur les effets des changements climatiques peuvent être trompeurs, si on ne tient pas compte de la mortalité des poissons due à la pêche. Les prédictions des

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modèles d'écosystèmes sont aussi affectées par l'importance relative des effets physiques directs et indirects sur les niveaux trophiques moyens et supérieurs.

[Traduit par la Rédaction]

Introduction

The ability of physical processes to structure ecosystems must be considered when measuring the top-down effects of fishing. We used a food-web model to explore how climate might affect the pelagic ecosystem in the eastern tropical Pacific Ocean (ETP). Previous workers have studied predator–prey interactions in the ETP (e.g., Olson and Boggs 1986; Robertson and Chivers 1997), but how these interactions structure the pelagic food web during climate variation has not been described.

Plant and animal populations in the ETP are affected by the El Niño – Southern Oscillation (ENSO). Several workers have documented a connection between the ENSO and both the rate of primary production and phytoplankton biomass in the ETP. The production rate is generally decreased during warm El Niño periods and increased during cold La Niña periods (e.g., Barber and Chavez 1983; Fiedler et al. 1992; Barber et al. 1996). Phytoplankton biomass can also be reduced during El Niños and increased during La Niñas (e.g., Fiedler et al. 1992; Barber et al. 1996; Bidigare and Ondrusek 1996). In addition to affecting plant productivity and biomass, the ENSO affects the species composition of the phytoplankton. In general, the ENSO affects the biomass of large (>5 μm) phytoplankton more than that of small (≤5 μm) phytoplankton (e.g., Bidigare and Ondrusek 1996; Landry et al. 1996). The ENSO also affects animals at middle and upper trophic levels. For example, Barber and Chavez (1983) concluded that the 1982–1983 El Niño reduced the growth rates and reproductive successes of various birds, mammals, and fishes.

Several coupled ocean-atmosphere models describe how the ENSO might respond to increased atmospheric concentrations of greenhouse gases during the 21st century. These models generally predict that mean sea-surface temperatures (SSTs) in the tropical Pacific Ocean will increase, but they do not agree on the future frequency and amplitude of ENSO cycling in the ETP. Timmermann et al. (1999) and Collins (2000*a*) predict an increase in both the amplitude and frequency of the ENSO, but Collins et al. (2001) do not predict significant changes in these statistics. Alternative hypotheses about the consequences of greenhouse warming for SSTs may lead to different predictions about the future structure of the pelagic ecosystem.

Our work has three objectives. The first is to explore how a single, ENSO-scale climate pulse might affect the middle and upper trophic levels of the pelagic ecosystem in the ETP. Second, we explore how the ecosystem might respond to changes in the periodicity of warm and cold events during sustained ENSO-scale cycling. Finally, we explore how greenhouse warming might affect the pelagic ecosystem in the ETP. We address these three objectives by simulating physical forcing events in a food-web model developed by Olson and Watters (2003). Although the focus of our work is on the ETP, we believe that many of our results can be generalized to other pelagic marine ecosystems.

Methods

System and model descriptions

We used a model developed and documented by Olson and Watters (2003). This model was assembled in Ecopath with Ecosim (EwE) (Walters et al. 2000) and contains 38 components (Table 1). Some components are split into two biomass pools based on length (Table 1). We identify the large and small fishes from these split pools with the respective abbreviations "Lg" and "Sm". Substantial uncertainty surrounds many of the parameters in Table 1. The model focuses on pelagic regions of the ETP, and coastal ecosystems are not adequately described.

Temporal dynamics in Ecosim are largely controlled by food consumption. Walters et al. (2000) provide the equations used in Ecosim, but we condense and reparameterize some of them here. Consumption (C_{ijt}) of prey i by predator j at time t depends on the biomasses of both the prey (B_{it}) and predator (B_{jt}) and can be influenced by environmental conditions:

$$(1) \qquad C_{ijt} = \frac{a_{ij} v_{ij} v^*_{ijt} B_{it} B_{jt}}{2v_{ij} v^*_{ijt} + a_{ij} B_{jt}}$$

where a_{ij} is the effective rate at which predator j searches for prey i and v_{ij} is the maximum instantaneous rate of mortality that predator j can impose on prey i; v^*_{ijt} can vary with environmental conditions and is an anomaly in v_{ij} at time t. The product of v_{ij} and v^*_{ijt} describes the vulnerability of prey i to predation by predator j at time t.

The recruitment (R_{it}) of components split into pools of large and small animals can also be affected by environmental conditions (again, Walters et al. (2000) provide detail about the recruitment function).

$$(2) \quad R_{i\,t+1} = f\left(R_{i\,t=0}, \frac{N^{\mathrm{Lg}}_{it}}{N^{\mathrm{Lg}}_{i\,t=0}}, \frac{\sum_j C^{\mathrm{Lg}}_{jit}}{B^{\mathrm{Lg}}_{it}}, p_{it}, \frac{\sum_j C^{\mathrm{Lg}}_{ji\,t=0}}{B^{\mathrm{Lg}}_{i\,t=0}}, q_{i\,t=0}\right) r^*_{it}$$

Time zero ($t = 0$) refers to the initial conditions described by the parameters in Table 1. $R_{i\,t=0}$ is a baseline recruitment estimated from these parameters. N^{Lg}_{it} is the simulated abundance of large fish in component i at time t, and B^{Lg}_{it} is their biomass. p_{it} is the time-specific proportion of energy that large fish allocate to reproduction, and $q_{i\,t=0}$ is the proportion of energy that large fish allocate to growth under the initial conditions (note that $q_{i\,t=0} \neq 1 - p_{it}$). r^*_{it} is a time-specific anomaly in the production of eggs (or larvae) that is independent of the biomass of large fish from component i and may be controlled by environmental conditions.

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Table 1. Parameters for the Ecopath model of the pelagic ecosystem in the eastern tropical Pacific (ETP) (Olson and Watters 2003).

Component (code for DP)	FL	TL	*B*	*Z*	*Q/B*	EE	DP	LD
Lg marlins[b]	≥150	5.3	**573**	1.00	7.80	0.50	SYFT (0.25)	×
Toothed whales[b]		5.2	31 000	0.02	6.75	**0.00**	CEPH (0.65)	×
Lg bigeye[a]	≥80	5.2	9 000	0.76	13.03	**0.33**	CEPH (0.71)	×
Sm marlins[b]	<150	5.2	**145**	0.50	9.00	0.75	*Auxis* (0.20)	×
Sm sharks[b]	<150	5.2	**270**	0.58	9.16	**0.58**	SYFT (0.40)	×
Spotted dolphins[a]		5.0	3 500	0.04	16.50	**0.22**	CEPH (0.60)	×
Lg swordfish[a]	≥150	5.0	**33**	0.44	7.80	0.75	CEPH (0.60)	×
Lg sailfish[a]	≥150	4.9	**52**	1.15	7.80	0.25	MMF (0.37)	×
Lg wahoo[a]	≥90	4.9	1 100	1.20	9.76	**0.07**	*Auxis* (0.23)	×
Lg sharks[b]	≥150	4.9	400	0.32	7.81	**0.48**	MEF (0.39)	×
Pursuit birds[a]		4.8	600	0.08	65.70	**0.23**	FLY (0.55)	
Lg yellowfin[a]	≥90	4.7	6 500	2.35	15.60	**0.36**	*Auxis* (0.54)	×
Sm dorado[a]	<90	4.7	2 000	3.15	27.40	**0.99**	FLY (0.44)	×
Mesopelagic dolphins[a]		4.6	17 000	0.04	16.50	**0.19**	MMF (0.54)	×
Lg dorado[a]	≥90	4.6	**218**	1.20	21.90	0.25	FLY (0.55)	×
Skipjack[b]		4.6	**26 443**	1.88	21.50	0.40	MEF (0.31)	×
Albacore		4.6	**3 026**	0.77	16.95	0.75	MEF (0.54)	×
Sm yellowfin[a] (SYFT)	<90	4.6	8 200	1.75	18.30	**0.92**	MEF (0.37)	×
Sm sailfish[a]	<150	4.6	**127**	0.57	9.76	0.75	MMF (0.42)	×
Sm wahoo[a]	<90	4.6	**2 730**	1.75	11.40	0.75	MEF (0.48)	×
Sm bigeye[a]	<80	4.5	10 000	0.72	15.25	**0.69**	MMF (0.58)	×
Bluefin[a]		4.4	1 400	0.65	12.80	**0.80**	MEF (0.20)	×
Sm swordfish[a]	<150	4.4	**98**	0.21	9.00	0.75	MEF (0.66)	×
Cephalopods[c] (CEPH)		4.4	**1 104 807**	2.00	7.00	0.85	MMF (0.42)	
Misc. piscivores[a]		4.3	**16 536**	2.25	7.73	0.95	MEF (0.43)	×
Auxis[c]		3.9	**143 247**	2.50	25.00	0.95	MESZ (0.48)	×
Grazing birds[a]		3.8	123	0.15	65.70	**0.13**	MESZ (0.39)	
Baleen whales[a]		3.8	9 100	0.02	9.10	**0.00**	MESZ (0.84)	
Rays[a]		3.7	230	0.25	3.91	**0.36**	MESZ (0.45)	×
Sea turtles[a]		3.6	**260**	0.15	3.50	0.50	MESZ (0.47)	×
Crabs[a]		3.5	**119 694**	3.50	10.00	0.95	MESZ (0.46)	
Flyingfishes[a] (FLY)		3.4	**160 604**	2.88	25.78	0.95	MESZ (0.60)	
Misc. mesopelagic fishes[a] (MMF)		3.4	2 000 000	2.00	10.78	**0.95**	MESZ (0.64)	
Misc. epipelagic fishes[b] (MEF)		3.2	**2 248 549**	2.07	10.78	0.95	MESZ (0.48)	×
Mesozooplankton (MESZ)		2.7	**706 709**	64.00	200.00	0.68	MICZ (0.70)	
Microzooplankton (MICZ)		2.0	**826 425**	143.00	600.00	0.98	SP (1.00)	
Lg phytoplankton		1.0	**426 093**	125.00		0.90		
Sm producers (SP)		1.0	**2 999 183**	167.00		0.99		

Note: Some parameters are not provided because of space limitations, but the full set can be obtained from the authors. FL, fork length (cm); TL, trophic level; *B*, biomass (t·million km^{-2}); *Z*, total mortality rate; *Q/B*, consumption to biomass ratio; EE, ecotrophic efficiency; DP, dominant prey in the ETP (proportion of diet); LD, landed or discarded by fisheries in the ETP; Lg, large; Sm, small; Misc., miscellaneous. Values in bold type were estimated by solving the Ecopath mass-balance equations.

[a]The mass-balance solution is relatively insensitive to variation in the parameters for these components (Olson and Watters 2003).

[b]The mass-balance solution is moderately sensitive to variation in the parameters for these components (Olson and Watters 2003).

[c]The mass-balance solution is highly sensitive to variation in the parameters for these components (Olson and Watters 2003).

Physical forcing of phytoplankton biomass

We used variations in the biomass of large phytoplankton to drive our ecosystem model from the bottom up. We assumed that the ENSO causes variability in the biomass of large phytoplankton, but not in the biomass of small producers. This assumption is consistent with observations that the biomass of diatoms varied substantially during recent warm and cold events, whereas the biomass of picoplankton was relatively stable (Bidigare and Ondrusek 1996; Landry et al. 1996). The effect of assuming that the biomass of small producers did not vary with the ENSO was to decrease the amplitude of bottom-up effects in our simulations.

We created time series of $B_{\text{Lg phytoplankton } t}$ with an empirical model that relates the SST anomolies of the NIÑO3 region (5°N–5°S, 150–90°W) to surface chlorophyll concentrations. During recent warm and cold events, log(pigment concentrations (mg·m^{-3})) in the NIÑO3 region changed by about –0.109/°C (the mean of the rightmost column of values in Table 2). We used this estimate to create time series of large phytoplankton biomass that were representative of ENSO-scale forcing.

$$B_{\text{Lg phytoplankton } t} = B_{\text{Lg phytoplankton } t=0} \cdot \exp(-0.109X_t) \quad (3)$$

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Table 2. Phytoplankton-pigment data and NIÑO3 sea-surface temperature (SST) anomalies used to construct eq. 3.

Source of chlorophyll data	Time periods	Mean pigment concentration ($mg \cdot m^{-3}$) in model arena (P)	Mean NIÑO3 SST anomaly (°C) (T)	Change in log(pigment concentration) per °C $(\ln(P_2/P_1)/(T_2 - T_1))$
Shipboard observations (Fiedler et al. 1992)	(1) Aug.–Nov. 1987	$P_1 = 0.130$	$T_1 = +1.71$	–0.169
	(2) Aug.–Nov. 1988	$P_2 = 0.222$	$T_2 = -1.45$	
Monthly coastal zone color scanner data (Tran et al. 1993)	(1) Jan.–April 1983	$P_1 = 0.081$	$T_1 = +2.65$	–0.100
	(2) Jan.–April 1984	$P_2 = 0.106$	$T_2 = -0.05$	
Monthly SeaWiFS data (http://seawifs.gsfc.nasa.gov/SEAWIFS.html)	(1) Nov. 1997 – May 1998	$P_1 = 0.124$	$T_1 = +2.79$	–0.058
	(2) Nov. 1998 – May 1999	$P_2 = 0.151$	$T_2 = -0.61$	

Note: The SST anomalies were obtained from the United States National Oceanic and Atmospheric Administration, National Weather Service, Climate Prediction Center, and cover the NIÑO3 area (5°N–5°S, 150–90°W).

$B_{\text{Lg phytoplankton } t=0}$ is the biomass of large phytoplankton from Table 1, and X_t is a NIÑO3 SST anomaly at time t. To generate biomass trajectories for large phytoplankton, we entered various time series of SST anomalies (see Simulations) into eq. 3. We used these biomass trajectories to drive the ecosystem model by appropriate substitution of $B_{\text{Lg phytoplankton } t}$ for B_{it} in eq. 1. Thus, we forced the biomass of large phytoplankton to decrease during warm events and increase during cold events. Equation 3 is not suitable for coastal regions of the ETP.

Physical forcing of predator recruitment

Forcing our model via eq. 3 can cause predator biomasses to decrease after a warm event, but estimates from Maunder and Watters (2002) suggest that annual recruitments of yellowfin tuna were highest following the 1987 and 1998 El Niños. We addressed this inconsistency with two other empirical models. These two models relate predator recruitment to NIÑO3 SST anomalies and force recruitment to increase during warm events. We forced recruitment to all of the split-pool components except sharks. Shark recruitment was not forced because the shark species represented by our model are viviparous or ovoviviparous. We assumed that environmental effects on recruitment to populations with reproductive modes involving parental care are different from those on oviparous fishes. The effect of this assumption was that sharks did not benefit from warm events as much as other predators.

We hypothesized that environmental conditions might affect the recruitment of predators in split pools by influencing both survival of small fishes and egg production by large fishes. The former type of forcing is consistent with an untested hypothesis that increased growth rates during warm events cause small predators to spend less time inside a window of increased vulnerability to predation. Physical forcing of egg production is consistent with observed relationships between spawning activity by yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tunas and SST (Schaefer 1998, 2001).

To specify temporal trends in vulnerability to predation, we first obtained a single estimate of v_{ij} for all predator–prey links in our model (i.e., we assumed that $v_{ij} = v \; \forall \; i$ and j). We estimated this parameter by fitting to 28 time series of relative abundance and four time series of total mortality (Z) estimates. Some of the abundance indices were generated from the output of single-species stock assessments (large and small yellowfin, large and small bigeye, large and small marlins, albacore, and skipjack) and others were derived from catch-per-unit-effort (CPUE) data (large and small marlins, large and small sharks, large and small sailfish, large swordfish, small dorado, small wahoo, miscellaneous piscivores, rays, sea turtles, and miscellaneous epipelagic fishes). The time series of Zs were obtained from single-species stock assessments (large and small yellowfin and bigeye). We estimated that predators could increase the instantaneous rate of predation mortality on their prey to about 1.8 times the rates implied by the parameters in Table 1. With this estimate, our model provided relatively good fits to the stock-assessment data and relatively poor fits to the CPUE data. We were not disappointed by the lack of fit to the CPUE series because it was not likely that variations in the CPUE data reflected actual

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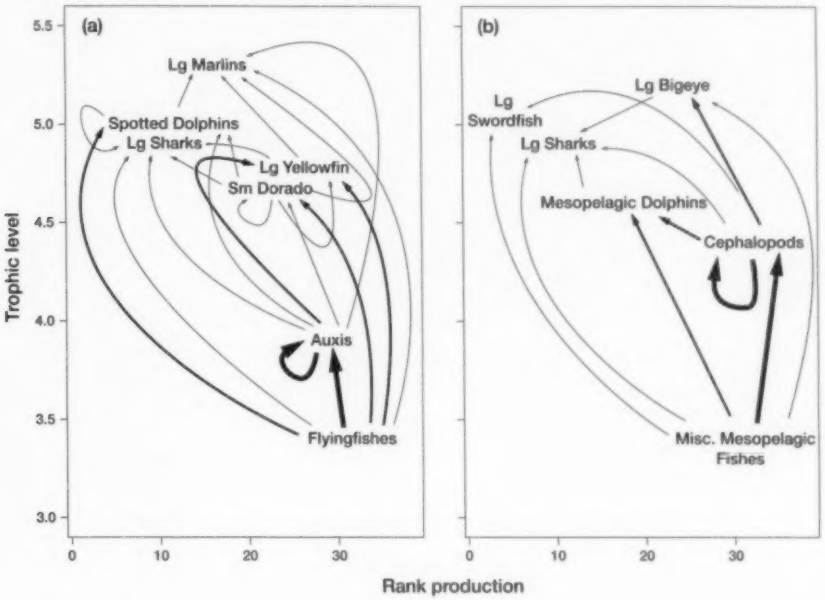
Fig. 1. Schematic representations of (*a*) the axis of the *Auxis* and (*b*) the axis of the squid. These two axes were defined for the purpose of summarizing our results. Thin arrows indicate that <1% of the total biomass flowing within an axis is being transferred between two components. Arrows of medium thickness indicate that 1–25% of the total biomass flowing within an axis is being transferred, and thick arrows indicate that >25% of the total flow is occurring between two components. Rank production was calculated for all of the components in the ecosystem model (Table 1). Lg, large; Sm, small; Misc., miscellaneous.



variations in biomass. Rather, these variations were probably the result of changes in catchability and availability. We also note that Olson and Watters (2003) estimated v_{ij} by fitting only to the stock-assessment data for yellowfin and bigeye tunas. Their estimate was similar to ours, and this similarity implies that the CPUE data used here contained relatively little information about vulnerability.

We also generated series of v^*_{ijt} to force temporal trends in predator vulnerability. We used estimates of recruits per spawner from a recent stock assessment of yellowfin tuna (Maunder and Watters 2002) to obtain (via maximum likelihood) the rate parameter of an empirical model describing how vulnerability to predation might vary with changes in SST.

$$(4) \qquad v^*_{ijt} = \exp(-1.271X_t)$$

where $i \in$ {Sm marlins, Sm dorado, Sm yellowfin, Sm sailfish, Sm wahoo, Sm bigeye, Sm swordfish}. We generated series of v^*_{ijt} by entering NIÑO3 SST anomalies (see Simulations) into eq. 4, and we used these series of v^*_{ijt} to drive the ecosystem model by appropriate substitution into eq. 1. Thus, we forced small predators from split-pool components to be less vulnerable to predation during warm events and more vulnerable during cold events.

We also used the stock-assessment information from Maunder and Watters (2002) to develop an empirical model of how egg production by large fishes in split-pool components might be influenced by SST. We obtained a maximum likelihood estimate of the rate parameter for this model by fitting to data on relative recruitment (time-specific recruitments divided by an average recruitment).

$$(5) \qquad r^*_{it} = \exp(-0.131X_t)$$

where $i \in$ {Sm marlins, Sm dorado, Sm yellowfin, Sm sailfish, Sm wahoo, Sm bigeye, Sm swordfish}. We generated series of r^*_{it} by entering NIÑO3 SST anomalies into eq. 5, and we substituted these series of r^*_{it} into eq. 2. Thus, we forced egg production to increase during warm events and decrease during cold events.

Simulations

We used eqs. 3–5 to construct two scenarios by which physical forces affect the pelagic ecosystem in the ETP. We use the term scenario because eqs. 3–5 are correlative, not mechanistic. For scenario 1, we used only eq. 3 to drive the ecosystem. Scenario 1 modeled only bottom-up forcing of large phytoplankton biomass, and we categorized the effects of this scenario on middle and upper trophic levels as indirect. For scenario 2, we used eqs. 3–5 simultaneously. Scenario 2 modeled the combined effects of forcing large phytoplankton biomass and predator recruitment. We categorized environmental effects on recruitment as direct, and therefore, scenario 2 included both indirect and direct environmental effects on components at middle and upper trophic levels. Comparing the results of simulations forced under scenario 1 with those forced under scenario 2 allowed us to consider interactions between the indirect and direct effects of physical forcing.

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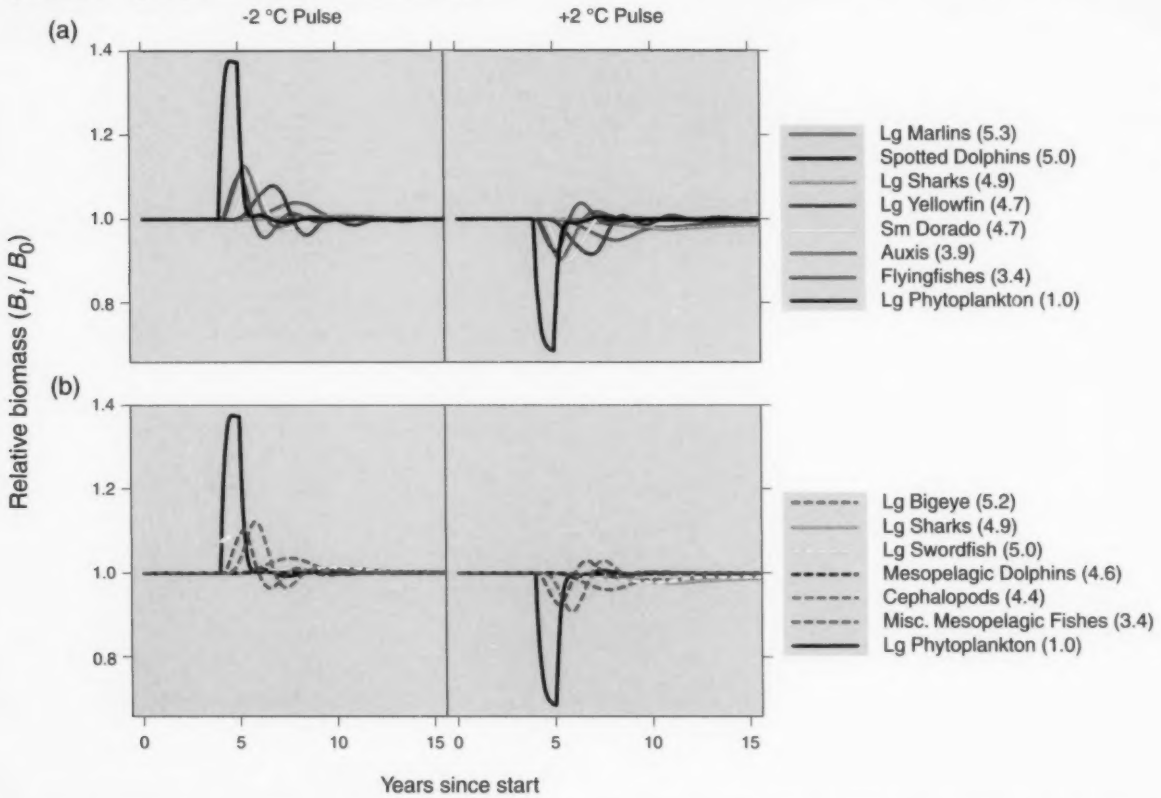
Fig. 2. Simulated effects, under scenario 1, of single pulses in the biomass of large phytoplankton corresponding to ±2 °C pulses in sea-surface temperature. The trophic level of each component from (*a*) the axis of the *Auxis* and (*b*) the axis of the squid is indicated in parentheses. Lg, large; Sm, small; Misc., miscellaneous.



We ran three sets of simulations under each scenario. In the first set, we substituted positive and negative climate-anomaly pulses (±2 °C SST anomalies) for X_t in eqs. 3–5. We chose these anomalies because they span the dynamic range of most anomalies observed in the NIÑO3 time series. Each pulse was specified to occur for 1 year during a 50-year simulation.

In the second set of simulations, we substituted regular climate cycles (corresponding to alternating ±2 °C SST anomalies) for X_t in eqs. 3–5. We considered ENSO-scale cycles with 2-, 4-, and 6-year periods and with "early", "even", and "late" cadences. We defined cadence according to the relative position of a cold event within a single warm–cold cycle. Cycles with even cadence had a cold event occurring exactly halfway between two successive warm events. Early cadence was when the cold event occurred during the first half of a cycle, and late cadence was when the cold event occurred during the second half of a cycle. We structured the second set of simulations so that one cold event always fell between successive warm events.

In the final set of simulations, the ecosystem was driven with NIÑO3 SST anomalies predicted from three models of greenhouse warming. We used means of winter (November–March) anomalies predicted from the Max Planck global climate model (GCM; referred to as the ECHAM4/OPYC3 coupled general circulation model by Timmermann et al. (1999)) and the second and third versions of the Hadley Centre coupled model (HadCM2 from Collins (2000*a*); HadCM3 from Collins et al. (2001)). The ENSO signals in these global-warming scenarios are complex. There are subtle changes in both the frequency and cadence of warm and cold events, and there are successive warm events without intervening cold events (and vice versa). The global-warming scenarios are further characterized by long-term increases in SST. Using eqs. 3–5, we translated these trends into long-term reductions in large phytoplankton biomass and increases in predator recruitment. We used winter SST anomalies in this set of simulations because our work focused on interannual change, and in the ETP, ENSO-induced variations in SST are typically amplified during this season.

Fishing mortality rates (F) were specified for each set of simulations. In the first two sets, Fs were constant and equal to the average F estimated to have affected each component during 1993–1997 (the Fs that Olson and Watters (2003) used to compute a mass balance). Two levels of F were used in the third set of simulations: F = average F during 1993–1997, and F = 0. Components that were subjected to F are listed in Table 1, and uncertainty surrounds the average Fs that we used.

We summarized our results by focusing on two subsets of components from the ecosystem. We named these subsets "axis of the *Auxis*" and "axis of the squid". The trophic

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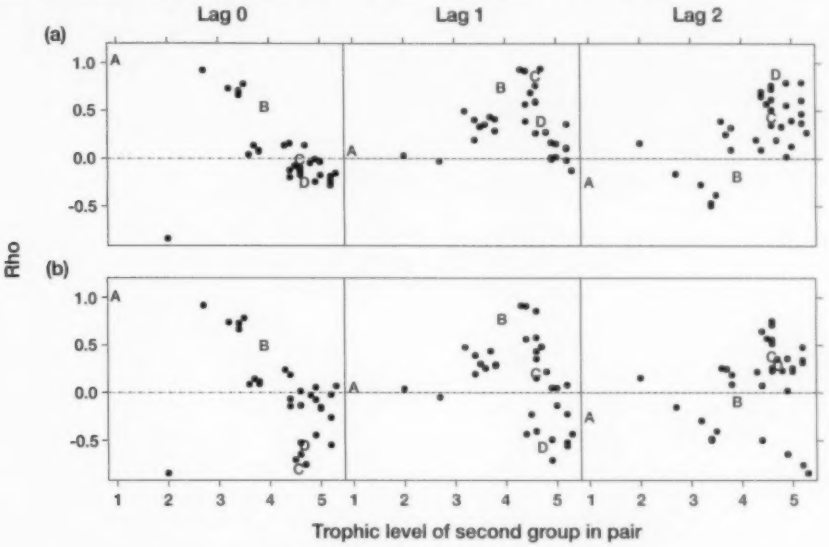
Fig. 3. Spearman rank correlations (rho) between large phytoplankton and all other components of the ecosystem. The model was forced with an historical series (1900–1999) of NIÑO3 sea-surface temperature anomalies. Correlations were computed at lags of 0, 1, and 2 years. (*a*) Results from scenario 1; (*b*) results from scenario 2. The points marked "A" are large phytoplankton – large phytoplankton correlations; the points marked "B" are large phytoplankton – *Auxis* correlations; the points marked "C" are large phytoplankton – small yellowfin correlations; and the points marked "D" are large phytoplankton – large yellowfin correlations. The solid dots are correlations between large phytoplankton and all other components of the ecosystem.



pathways within these subsets are illustrated in Fig. 1. We chose these subsets for four practical reasons. First, each axis includes predators that are of interest from both utilization and conservation perspectives (e.g., large yellowfin and large sharks). Second, the components within each axis have simulated biomass trajectories that bracket the dynamic range of the responses that we predicted (e.g., *Auxis* and cephalopods trajectories were highly variable). Third, the components within each axis illustrate patterns and trends that were representative of groups not included in either axis (e.g., trends for flyingfishes were representative of those for miscellaneous epipelagic fishes). Finally, there are direct trophic linkages, including cannibalism, between the components of each axis (e.g., large bigeye eat cephalopods, and cephalopods are cannibalistic). The axes represent two pathways by which energy derived from bottom-up forcing can flow to the middle and upper trophic levels, but these axes are not alternative system states.

Results

ENSO-scale effects from scenario 1

Bottom-up pulses of large phytoplankton biomass, corresponding to ±2 °C SST anomalies, caused the biomasses of most ecosystem components to oscillate (Fig. 2). These oscillations often propagated for years after the pulse. Responses to pulses in large phytoplankton biomass were related to trophic level, but not to whether ecosystem components were members of the axis of the *Auxis* or the axis of the squid. Pulse-induced variations in biomass were greatest for components at middle trophic levels (e.g., flyingfishes, *Auxis*, small dorado, miscellaneous mesopelagic fishes, and cephalopods) and lowest for components at upper trophic levels (e.g., large sharks, large swordfish, and large marlins). In general, responses to bottom-up pulses were lagged, and the lag increased with increasing trophic level. For some components at high trophic levels, the effects of negative bottom-up pulses (positive SST anomalies) were longer in duration than those of positive bottom-up pulses (negative SST anomalies). Marine mammals did not respond to bottom-up pulses, and pulses did not kick the system into alternative states (all biomass trajectories eventually returned to their initial conditions).

We further examined lags in responses to bottom-up forcing with an historical series (1900–1999) of winter mean NIÑO3 SST anomalies computed from data provided by Kaplan et al. (1998) and Reynolds and Smith (1994). We obtained these data from the LDEO/IRI Data Library at http://ingrid.ldeo.columbia.edu. We computed pairwise correlations between large phytoplankton biomass and the biomasses of all other components at lags of 0, 1, and 2 years. Lower trophic levels were correlated with the large phytoplankton at short lags; middle trophic levels were correlated with the large phytoplankton at medium lags; and upper trophic levels were correlated with the large phytoplankton at long lags (Fig. 3). Bottom-up effects acted as trophic waves that propagated through the ecosystem.

Changing the period and cadence of regular cycles in large phytoplankton biomass affected the oscillatory patterns of biomass trajectories for components at middle and upper trophic levels. As the period of bottom-up cycles increased, the period of cycles in other ecosystem components also increased (Fig. 4). Increasing the period of warm–cold cycles also caused the trajectories of some ecosystem components (e.g., flyingfishes and small dorado) to become mixtures of waves with different amplitudes (Fig. 4). As with bottom-up

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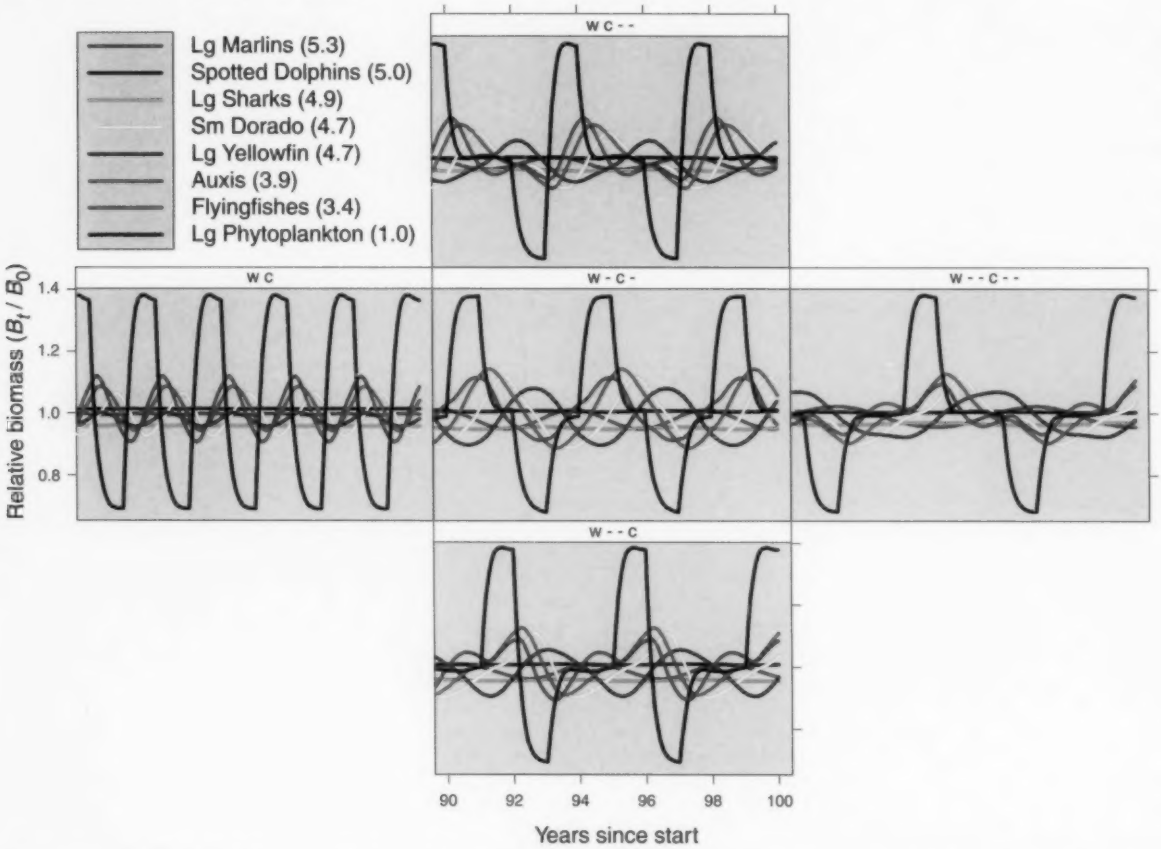
Fig. 4. Simulated effects, under scenario 1, of regular, warm–cold cycles on components in the axis of the *Auxis*. The heading at the top of each panel indicates the structure of the cycle that was used to force the model. "W" indicates warm events (2 °C sea-surface temperature (SST) anomalies), "C" indicates cold events (–2 °C SST anomalies); and dash (–) indicates average conditions (0 °C SST anomalies). Panels in the middle row illustrate simulations with 2-, 4-, and 6-year periods (from left to right); the climate drivers for all of these simulations had even cadences. Panels in the middle column illustrate simulations with "early", "even", and "late" cadences (from top to bottom); all of these simulations had forcing with a 4-year period. The trophic level of each component is indicated in parentheses. Lg, large; Sm, small.



pulses, the amplitudes of these oscillations decreased with increasing trophic level. Changing the period of ENSO-scale cycles in the biomass of large phytoplankton had small, but seemingly biologically insignificant, effects on the means and variances (computed over a single cycle) of the biomass trajectories for other components in the model (results not shown). Changing the cadence of the bottom-up forcing affected animals at middle and upper trophic levels in a manner similar to that of changing the period. Although most biomass trajectories were sensitive to the period and cadence of ENSO forcing, none of the cyclic-forcing simulations predicted that the ecosystem would be restructured by the extinction or explosion of one or more components (Fig. 4).

ENSO-scale effects from scenario 2

Forcing under scenario 2 changed both the short- and long-term predictions from our ecosystem model. The short-term effect was that the biomasses of all split-pool components (except sharks because they were not forced under scenario 2) increased immediately after a reduction in large phytoplankton biomass (a warm event) (Fig. 5). After this increase, the biomasses of split-pool components declined, and the trajectories fell into phase with the predictions made under scenario 1 (Fig. 5). The long-term effect of forcing under scenario 2 was to increase variability in the biomass trajectories of split-pool components (Fig. 5). When the historical series (1900–1999) of NIÑO3 SST anomalies was used to force the model, the ecosystem was not restructured by split-pool components that either capitalized on a series of warm events or suffered from a series of cold events (Fig. 5). Negative correlations between the biomasses of large phytoplankton and components at upper trophic levels were more common under scenario 2 than scenario 1 (Fig. 3).

Global-warming effects

We reiterate that the SST anomalies used to drive the set of global-warming simulations contain complex combinations of ENSO periods and cadences superimposed on long-term

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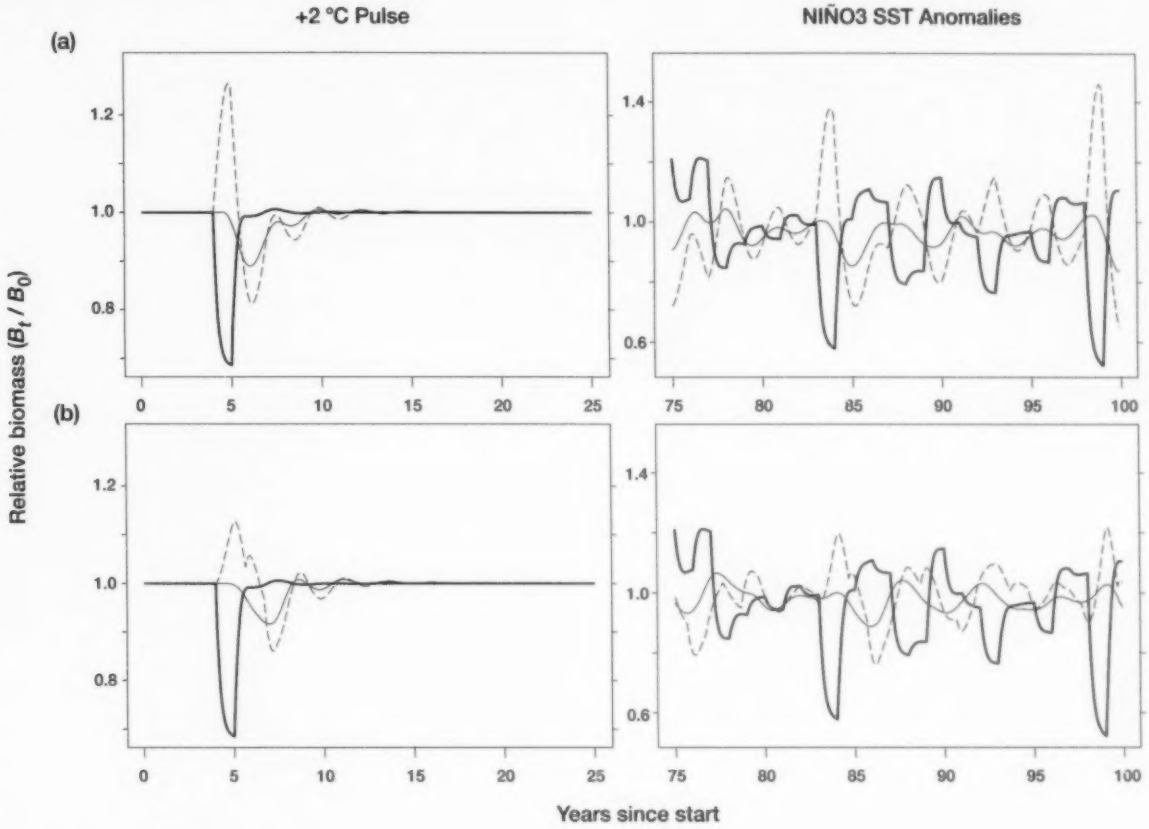
Fig. 5. Biomass trajectories for large phytoplankton (thick solid lines) and yellowfin tuna predicted under scenarios 1 (thin solid lines) and 2 (thin broken lines). The panels in row (*a*) are for small yellowfin, and the panels in row (*b*) are for large yellowfin. SST, sea-surface temperature.



warming trends. To decouple the periodicity and warming effects, we analyzed the simulated biomass trajectories with wavelets (Torrence and Compo 1998). Although the Max Plank GCM, the HadCM2, and the HadCM3 predict different ENSO patterns (and therefore different estimates of biomass at any specific time), our wavelet analyses of the biomass trajectories predicted from these three climate models gave similar results. Therefore, all further references to the global-warming simulations are to the Max Planck GCM.

The time-averaged wavelet spectra of many biomass trajectories predicted from our global-warming simulations were characterized by significantly high power at periods of about 1.5–6 years (Table 3). The components with spectra displaying this feature were sensitive to ENSO-scale forcing during global warming. Significantly high power at short periods was typical of spectra from components with relatively high Zs (Table 3). These results were robust to the differences between scenarios 1 and 2, but forcing under scenario 2 caused some components with relatively low Zs (e.g., large marlins and large bigeye) to be sensitive to ENSO-scale forcing (Table 3). Components with Zs less than about 0.5 were not sensitive to ENSO-scale forcing during global warming (Table 3).

The time-averaged wavelet spectra of all biomass trajectories from the global-warming simulations were also characterized by a steady increase in power with increasing period (Table 3). This result was obtained under both forcing scenarios, and it illustrated the importance of the global-warming trend. Under scenario 1, long-term warming was predicted to reduce the relative biomasses of all ecosystem components (Fig. 6). These reductions were predicted regardless of whether the simulation included fishing mortality, but the absence of fishing mitigated the impact of warming on some predators (e.g., large sharks, large marlins, and large yellowfin) (Fig. 6). Under scenario 2, long-term warming was predicted to increase the relative biomasses of all split-pool components except sharks (Fig. 7). These components benefited from an increasing trend in recruitment.

We also used variance-components models to analyze the biomass trajectories predicted from the global-warming simulations. We treated the two levels of F used in these simulations (F = average F during 1993–1997, and F = 0) as random effects and estimated the fraction of the total variation in the two trajectories predicted for each component that was explained by differences in F. These variance ratios were estimated by maximum likelihood and ranged from 0

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Table 3. Characteristics of the time-averaged power spectra of various biomass trajectories predicted by forcing the ecosystem model with 21st century sea-surface temperature anomalies from the Max Planck global climate model.

	Significantly high power at periods of about 1.5– 6 years		Power increases as the period increases	
Component (*Z*)	Scenario 1	Scenario 2	Scenario 1	Scenario 2
Axis of the *Auxis*				
Spotted dolphins (0.04)			×	×
Lg sharks[a] (0.32)			×	×
Lg marlins (1.00)		×	×	×
Lg yellowfin (2.35)	×	×	×	×
Auxis (2.50)	×	×	×	×
Flyingfishes (2.88)	×	×	×	×
Sm dorado (3.15)	×	×	×	×
Lg phytoplankton[a] (125.00)	×	×	×	×
Axis of the squid				
Mesopelagic dolphins (0.04)			×	×
Lg swordfish (0.44)			×	×
Lg bigeye (0.76)		×	×	×
Cephalopods (2.00)	×	×	×	×
Misc. mesopelagic fishes (2.00)	×	×	×	×

Note: A red-noise spectrum (AR(1)) was used to determine significance at $\alpha = 0.10$. The ecosystem components are sorted by *Z*. Lg, large; Sm, small; Misc., miscellaneous.

[a]These components are members of both axes.

(for large phytoplankton) to levels greater than 0.9 (for predators like large sharks, large swordfish, large yellowfin, and large bigeye) (Table 4). We used the variance ratios to measure the degree to which fishing and physical forcing shaped the dynamics of each ecosystem component. We interpreted relatively low variance ratios as indicators of control by physical forces and relatively high ratios as indicators of control by fishing. Intermediate variance ratios were considered to be indicative of mixed control.

The degree to which each component of the ecosystem appeared to be controlled by fishing or physics was related to the ratio F/Z (where F = average F during 1993–1997, and Zs are from Table 1). In general, components that were subjected to little or no fishing mortality (e.g., flyingfishes, cephalopods, and miscellaneous mesopelagic fishes) were controlled by physical forces. Marine mammals were, however, an exception to the latter result, and mammals appeared to be controlled by a mix of physical forces and fishing. Fishery targets and dominant bycatch species (e.g., large yellowfin, large bigeye, large sharks, and large marlins) were controlled by fishing rather than physics (Table 4). These results were generally robust to the differences between scenarios 1 and 2, but the variance ratios predicted from forcing under scenario 2 were almost always less than those predicted by forcing under scenario 1 (Table 4).

Discussion

We do not claim that our ecosystem model can accurately predict future levels of biomass; too much uncertainty surrounds our parameter estimates. Nevertheless, Olson and Watters (2003) provide results indicating that the ETP model may be a useful tool for studying how physical variability influences food-web dynamics. From an initial sensitivity analysis, Olson and Watters (2003) determined that the mass-balance allocation of energy among model components was most sensitive to parameter values for the cephalopods and *Auxis*. Because there is also substantial uncertainty surrounding the parameters for cephalopods and *Auxis*, Olson and Watters conducted a second sensitivity analysis to consider whether changing the parameters for these two components would affect (1) time-series predictions from Ecosim and (2) the model's fit to time-series data on yellowfin and bigeye tunas. In the former case, Olson and Watters found that changing parameter values for cephalopods and *Auxis* affected the scaling of biomasses predicted by Ecosim but had negligible effects on the prediction of trends. In the latter case, Olson and Watters found that goodness of fit to the data on yellowfin and bigeye tunas was usually degraded by changing the parameters for cephalopods and *Auxis* (sums of squares were increased from 0.2 to 69.7%). In a few cases, the goodness of fit was increased, but the largest such increase represented only a 3.3% reduction in the sum of squares. In our opinion, the results of Olson and Watters (2003) suggest that our focus on variability in future biomass, rather than actual levels of biomass, is appropriate.

Indirect effects from ENSO-scale variability in plant biomass

Results from both the pulse-forcing and cyclic-forcing simulations suggested that the biomass trajectories of components at upper trophic levels are less sensitive to ENSO-scale changes in large phytoplankton biomass than those of components at middle trophic levels. To some degree, this result is trivial because energy is lost during transfer between trophic levels, but life-history differences also shape responses to bottom-up forcing. In the ETP, predators like sharks and marlins consume animals from a wide range of trophic lev-

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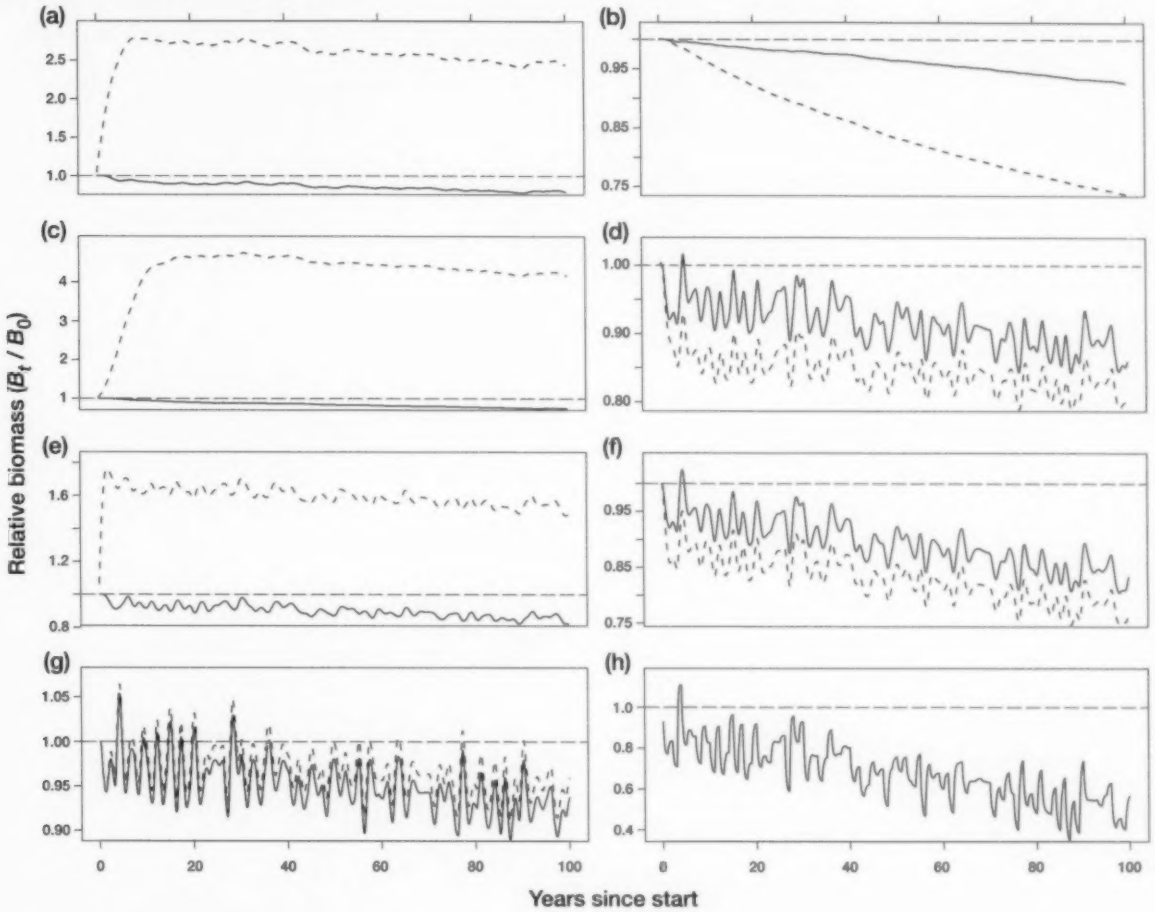
Fig. 6. The simulated effects, under scenario 1, of global warming on components in the axis of the *Auxis* ((*a*) large marlins, (*b*) spotted dolphins, (*c*) large sharks, (*d*) small dorado, (*e*) large yellowfin, (*f*) *Auxis*, (*g*) flyingfishes, and (*h*) large phytoplankton). The simulations were forced with winter mean sea-surface temperature anomalies predicted by the Max Planck global climate model. Solid lines are from simulations with F = average F during 1993–1997, and broken lines are from simulations with $F = 0$. A horizontal broken line is drawn for reference at $B_t/B_0 = 1.0$.



els (Olson and Watters 2003). These predators smooth through bottom-up variability by utilizing energy from different regions of the trophic pyramid. Some predators in the ETP, like dolphins, are also relatively unproductive, and despite having varied diets, their populations cannot respond quickly to short-term increases in bottom-up productivity. In contrast, components at middle trophic levels, like flyingfishes and cephalopods, prey on animals from a more narrow range of trophic levels and are highly productive. Less varied diets and high rates of productivity make components at middle trophic levels more sensitive to short-term changes in phytoplankton biomass.

Results from the pulse-forcing and cyclic-forcing simulations also showed how the bottom-up effects of individual climate events (e.g., El Niños and La Niñas) can be complicated by ecological interactions. Under scenario 1, biomass trajectories often trended in the opposite direction of the physical forcing because of combinations of interspecific (top-down) and intraspecific (density-dependent) effects. For example, a reduction in the biomass of flyingfishes was predicted to occur about 1 year after an increase in large phytoplankton biomass. Interspecific and intraspecific effects also caused many of the biomass trajectories predicted from the cyclic-forcing simulations to behave like complex mixtures of waves, despite the fact that our cyclic-forcing functions were simple.

It seems unlikely that one could monitor an individual population or stock (perhaps with stock assessments or research surveys) and determine whether individual peaks and valleys in a time series of biomass estimates resulted from bottom-up forcing. It takes time for variations in plant biomass to cascade through the system, and the lag of the response time is a function of each component's trophic level. To detect the indirect effects of climate on middle and upper trophic levels, one will need to monitor a suite of populations or stocks that are connected through predator–prey in-

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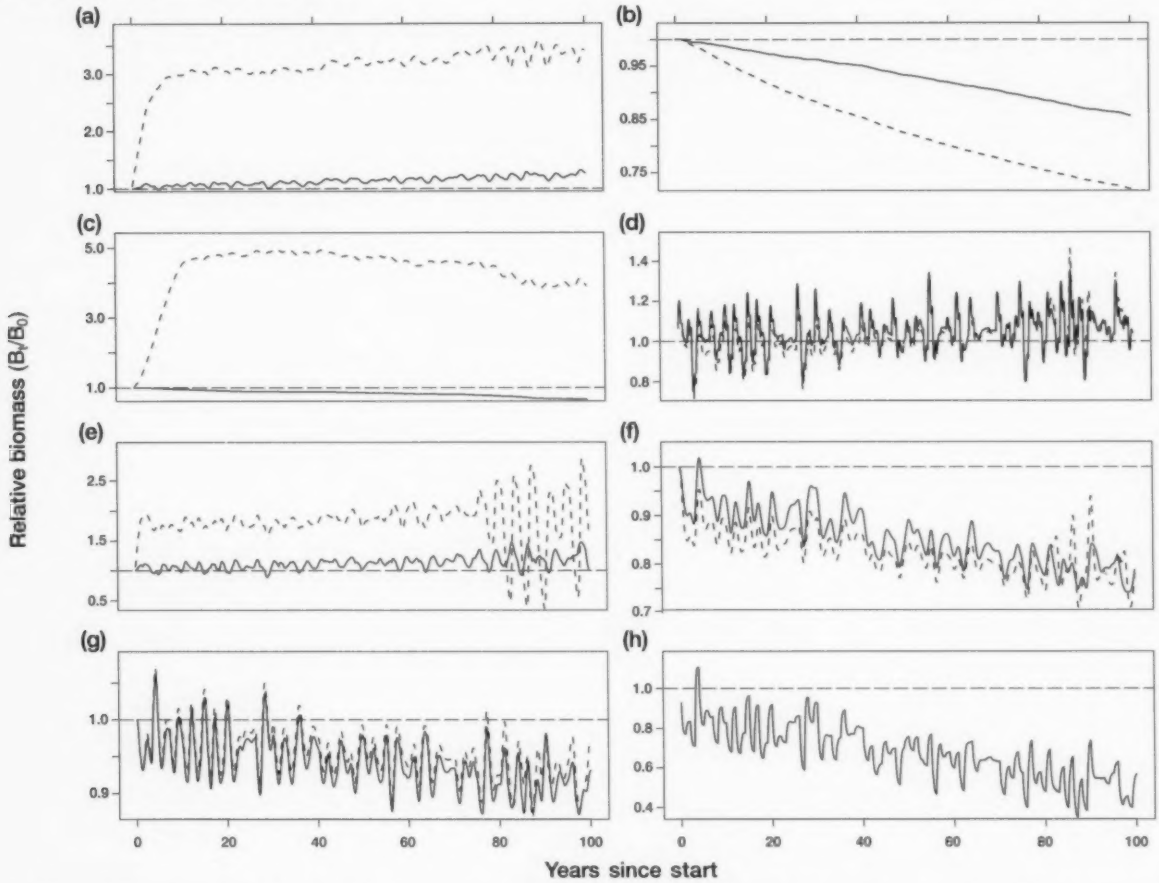
Fig. 7. The simulated effects, under scenario 2, of global warming on components in the axis of the *Auxis* ((*a*) large Marlins, (*b*) spotted dolphins, (*c*) large sharks, (*d*) small dorado, (*e*) large yellowfin, (*f*) *Auxis*, (*g*) flyingfishes, and (*h*) large phytoplankton). The simulations were forced with winter mean sea-surface temperature anomalies predicted by the Max Planck global climate model. Solid lines are from simulations with F = average F during 1993–1997, and broken lines are from simulations with $F = 0$. A horizontal broken line is drawn for reference at $B_t/B_0 = 1.0$.



teractions. Bottom-up signals can only be detected by their propagation through the food web.

Direct ENSO-scale effects

Comparing our results with those from the meta-analysis conducted by Micheli (1999) provides a useful background for discussing the importance of the direct effects of climate on middle and upper trophic levels. Although Micheli found a positive correlation between primary productivity and phytoplankton biomass, positive correlations between primary productivity and the biomasses of both mesozooplankton and zooplanktivorous fishes were found in only two of 20 pelagic marine systems. Micheli (1999) concluded that changes in primary productivity "rarely cascade upward to affect biomass of marine pelagic consumers". Our predictions from scenario 1, when considered jointly with previous observations of coupling between primary production and phytoplankton biomass in the ETP (e.g., Barber et al. 1996), were not consistent with this conclusion. In fact, scenario 1 predicted positive correlations between large phytoplankton biomass and the biomasses of most other components in the system, particularly if time lags were considered. Although it is not apparent that Micheli's meta-analysis considered time lags, we suggest that the absence of direct physical effects in scenario 1 is responsible for the apparent contradiction.

Micheli (1999) proposed three possible mechanisms to explain weak coupling between phytoplankton and herbivores; we offer a fourth possibility provoked by our predictions from scenario 2. We noticed that scenarios 1 and 2 predicted nearly identical correlations between large phytoplankton and components with trophic levels less than about 4.0. In contrast, the two mechanisms predicted less similar correlations between large phytoplankton and components with trophic levels greater than 4.0. Under scenario 1, all climate effects on upper trophic levels were indirect, but under scenario 2, 14 of the 25 components with trophic levels greater than 4.0 were also forced by direct effects on recruitment. We conclude that the relative strengths of indirect and direct physical effects can determine both the sign and scale of correlations between consumer groups and producer groups. Thus, a fourth way to explain Micheli's (1999) finding of

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Table 4. Variance ratios from the global-warming simulations.

Component (*F*/*Z*)	Scenario 1	Scenario 2
Axis of the *Auxis*		
Lg marlins (0.50)	0.97	0.95
Lg sharks[a] (0.48)	0.93	0.92
Lg yellowfin (0.35)	0.98	0.64
Spotted dolphins (0.03)	0.53	0.35
Sm dorado (0.01)	0.53	0.01
Auxis (0.00)	0.34	0.07
Flyingfishes (0.00)	0.10	0.04
Lg phytoplankton[a] (0.00)	0.00	0.00
Axis of the squid		
Lg swordfish (0.75)	0.92	0.91
Lg bigeye (0.31)	0.97	0.93
Mesopelagic dolphins (0.00)	0.55	0.44
Cephalopods (0.00)	0.02	0.00
Misc. Mesopelagic Fishes (0.00)	0.00	0.00

Note: Each ratio is the fraction of the total variation in two biomass trajectories (see Figs. 6 and 7) explained by the differences in fishing mortality (F = average F during 1993–1997, and $F = 0$). The ecosystem components are sorted by *F*/*Z*. Lg, large; Sm, small; Misc., miscellaneous.
[a]These components are members of both axes.

weak coupling between phytoplankton and herbivores is that herbivore populations are often subjected to direct physical effects on reproduction and growth, and these direct effects frequently dampen signals generated from bottom-up forcing. Our model does not currently include direct effects on consumers at low and middle trophic levels, but the literature contains references that recognize such effects in other systems influenced by the ENSO (e.g., Barber and Chávez 1986).

Our work suggests that under constant fishing mortality, direct physical effects are the dominant sources of interannual variation in the biomasses of consumer groups from the ETP. This statement hinges on our inclination to consider scenario 2 more realistic than scenario 1. We provide two reasons for this preference. First, given the discussion in the previous two paragraphs, scenario 1 seems less reasonable. Second, scenario 2 predicted a level of variation in small yellowfin biomass that was closer to the amount of variation in annual recruitment estimated for yellowfin tuna. The coefficient of variation (CV) in estimates of annual recruitment for yellowfin tuna is about 0.25 (Maunder and Watters 2002), and using winter mean NIÑO3 SST anomalies, CVs predicted from scenarios 1 and 2 were about 0.04 and 0.12, respectively.

It seems reasonable to ask how it is possible for predator recruitment to increase after an El Niño (e.g., Maunder and Watters 2002) despite observations of reduced phytoplankton biomass during these events (e.g., Barber et al. 1996). Presumably, even if large predators produce more eggs and small predators are themselves less vulnerable to predation, the recruits would still have to be supported by production from the bottom of the food web. In the ETP, it appears as if this support comes from the picoplankton. We did not model ENSO-driven changes in the biomass of small producers because measurements from flow cytometry (Landry et al. 1996) and estimates of the size fractionation of phytoplankton pigments (Bidigare and Ondrusek 1996) support the conclusion that there is less temporal variation in picoplankton biomass than in the biomasses of large cells like diatoms. These studies also show that picoplankton account for most of the plant biomass and production in the equatorial Pacific Ocean. The relatively large and temporally conservative biomass of picoplankton further supports our view that, given a constant level of fishing mortality, most of the interannual variations in the biomasses of consumer groups from the ETP are propagated by the direct, rather than indirect, effects of climate.

Global-warming effects

Regardless of how global warming affects the pattern of the ENSO, all components of the pelagic ecosystem in the ETP may be sensitive to long-term changes in the physical environment. Fishing may both mitigate and reinforce the effects of global warming. Sustained reductions in fishing mortality might mitigate the effects of global warming on components that are currently experiencing high levels of F relative to Z (e.g., large marlins, large sharks, and large yellowfin). The biomasses of other components (e.g., small dorado and *Auxis*) might be reduced by decreased levels of F because predation mortality on these components would be increased. Substantial reductions in F might also reduce the biomasses of components that feed on the same prey as the large fishes (e.g., spotted dolphins). Our results are consistent with a conclusion that has been made by other workers (e.g., Jurado-Molina and Livingston 2002): the effects of future climate change need to be considered in combination with future levels of fishing mortality.

Responses to global warming will also be affected by the degrees to which indirect and direct effects play a role in forcing the system. Direct, positive effects of global warming on predator recruitment can potentially compensate for a reduction in total plant biomass if some phytoplankton are not adversely affected by such climate change. In the ETP, the large and temporally stable biomass of picoplankton may provide the necessary base for consumers to profit from global warming. We note, however, that biogeochemical cycling and its effect on the bottom of the food web in the tropical Pacific Ocean is an area of active research, and future workers may find that picoplankton populations can be adversely affected by global warming.

The top-down effects of fishing

Although either bottom-up (e.g., Roemmich and McGowan 1995) or top-down (e.g., Shiomoto et al. 1997) processes may be the dominant mechanisms structuring marine ecosystems, it seems more robust to acknowledge that these processes act concomitantly (e.g., Verheye and Richardson 1998). In essence, bottom-up forces define a template on which top-down effects may act (Hunter and Price 1992; Power 1992). The effects of fishing are also constrained by this template, and we initiated this study because detecting the ecosystem consequences of fishing in the ETP will eventually require a description of the background variability in this system. Without such a description, we suspect that it will often be difficult to support hypotheses of fishing effects over hypotheses of environmental effects (and vice versa).

It seems likely that the fisheries operating in the ETP are able to control the biomasses of both target species (e.g., bigeye tuna) and bycatch species (e.g., sharks), even if physical variability is considered. Under recent levels of F, how-

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ever, some bycatch species (e.g., small dorado) are more likely to be controlled by physical forces. The degree to which fisheries control components of the ecosystem is partly determined by levels of F, but results from our variance-components analysis suggest that the top-down effects of fishing are less able to cascade through the food web if direct effects are the dominant source of physical variability in the system. This may be our most important conclusion.

Caveats and conclusions

Our results were sensitive to the rate parameters in eqs. 3–5, and such simple descriptions of physical–biological linkages may fail after additional data collection and analysis. Failures may occur because models like eqs. 3–5 are not mechanistic and may therefore oversimplify complex processes or describe spurious correlations. Nevertheless, the literature contains evidence supporting hypotheses that both phytoplankton biomass (see Introduction) and predator recruitment (see Methods) are affected by climate. Our estimates of the rate parameters determined both the scales of our predictions and the relative differences among the predictions from scenarios 1 and 2. We also assumed that the rate parameters in eqs. 3–5 are stationary. It seems reasonable to hypothesize that these rates would change over time, and further simulations with nonstationary rate parameters would be interesting.

Our use of EwE may have affected our conclusions. Projecting forward from a mass-balance "snapshot" may be misleading if the system was never actually in balance. Nevertheless, we found the approach amenable given that the data, particularly the diet compositions, used to parameterize the model were themselves snapshots. Two other aspects are perhaps more troublesome. First, models like ours that aggregate over large spatial scales, many species, and multiple age structures are likely to be less responsive to the effects of fishing than models with less aggregation (Cox et al. 2002). Responsiveness to environmental effects is also likely to be influenced by the level of aggregation in a model (Rice 1995), and it would be interesting to compare our results with those from models with different numbers of components. Second, although we investigated model uncertainty by considering two forcing scenarios, the predator–prey dynamics in EwE are limited to the family of behaviors that can be described by eq. 3. Rice (2001) notes that the effects of physical forcing need to be investigated in the context of consumer groups that participate in scramble competition (all consumers undergoing simultaneous periods of food shortage or excess). This appears to be particularly relevant to regime shifts. Regime shifts may occur in the ETP (McPhaden and Zhang 2002; Chavez et al. 2003), but we did not simulate this type of forcing. We acknowledge, therefore, that there are likely to be dynamic behaviors, both ecological and physical, that dampen or intensify the patterns described here.

Our global-warming simulations predicted considerable hypothetical changes in the upper trophic levels of the ecosystem, but these changes may not occur if populations can redistribute spatially. Most of the animals at upper trophic levels are mobile, and large-scale spatial displacements seem likely. For example, the distribution of skipjack tuna in the western Pacific Ocean is linked to large, zonal displacements of the equatorial warm pool (e.g., Lehodey et al. 1997). Range displacement may further complicate predictions about the effects of global warming because large-scale climate changes can also be expected at temperate latitudes (Meehl et al. 1993; Collins 2000*b*). Finally, despite the possibility of range shifts, genetic adaptation or physiological compensation to climate change may occur (Fields et al. 1993; Wood and McDonald 1997).

Our model focused on the ETP, but the following conclusions might be general. First, it will be difficult to detect bottom-up signals in biomass trajectories of single populations, and therefore, workers should look for such signals propagating through a set of biomass trajectories linked by predator–prey interactions. Second, physical forcing that acts directly on animals at middle and upper trophic levels (e.g., by affecting recruitment) can be the dominant source of interannual variability (given a constant level of F) in the biomasses of pelagic consumers. Following this, it seems likely that the top-down effects of fishing are less able to cascade through food webs that are dominated by direct physical effects. Finally, predictions about the effects of long-term climate change (e.g., global warming) on animals at middle and upper trophic levels may be misleading if future levels of F are not considered. In developing ecosystem models, it is critical to understand where physical forces interact with food webs (Rice 2001). Our results clearly illustrate that predictions from these models are sensitive to the relative strengths of indirect and direct physical effects on middle and upper trophic levels.

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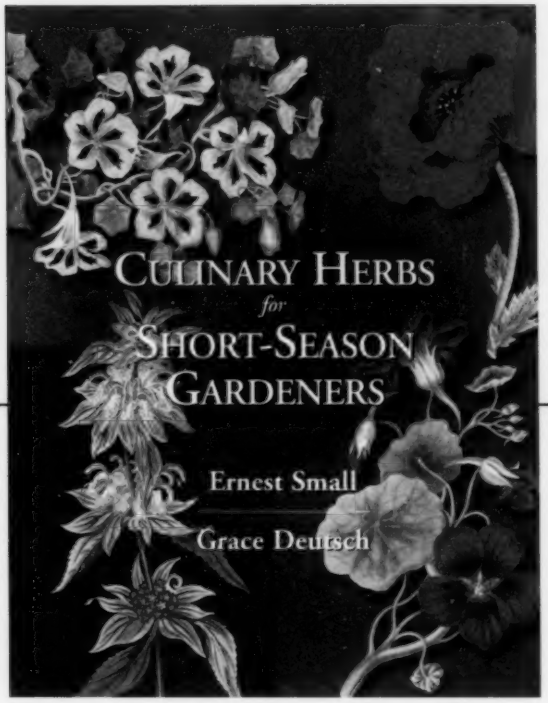

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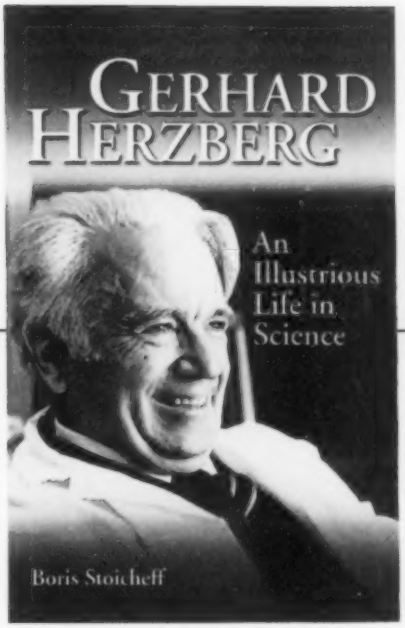

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